

Genetic variation in major phenotypic traits among diverse genetic origins of teak (*Tectona grandis* L.f.) planted in Taliwas, Sabah, East Malaysia

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Abstract

• **Introduction** As a forest species, genetic variability is high in teak (*Tectona grandis*) and domestication of the species is very recent. The selection effect among qualitative and quantitative traits is therefore expected to be strong. Native provenances and clonal seed orchard families were compared in this study.

• **Materials and methods** Forty-one genetic origins of teak, including 26 open-pollinated families from a clonal seed orchard in Ivory Coast, were planted in 1997 in a replicated trial at Taliwas, Sabah, East Malaysia.

• **Results and discussion** The mortality rate and early measurements of height, and diameter at breast height varied substantially between treatments. The largest height (>18 m) and diameter (>21 cm) values recorded after

104 months were mostly from the clonal seed orchard families, while the lower performances were mainly observed for the native provenances. Narrow sense heritabilities, assessed for the clonal seed orchard families only, increased gradually with age, reaching relatively high values, especially for height at 104 months ($h^2=0.76$). There were also some highly significant differences between the 41 genetic origins for six qualitative traits observed from 25 to 104 months. Overall, the clonal seed orchard families were marginally less crooked and grew more vertically than the other sources.

• **Conclusions** These findings provide further evidence of the usefulness of a clonal seed orchard phase in the genetic improvement of teak and the beneficial influence of a wet tropical climate on major economic traits.

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1 Introduction

Within the Verbenaceae family, the genus *Tectona* comprises four species: *Tectona grandis* L.f., *Tectona hamiltoniana* Wall, *Tectona philippinensis* Benth. & Hook.f., and *Tectona abludens* formerly identified as a sub-species of *T. grandis* (Kaosa-ard 1999). *T. grandis*, commonly known as teak, occurs naturally in India, Laos, Thailand, and Myanmar (ex-Burma) and is considered as sub-spontaneous in Indonesia, where it was introduced some 400–600 years ago (Kaosa-ard 2000; Siswamartana 2000). This large and long-lived tropical tree species is far more popular than the other three species in the genus due to the premium quality of its wood (Kadambi 1972; Keogh 2001; Tewari 1992). This accounts for the extensive establishment of plantations within and beyond its native range, especially since the beginning of the twentieth century (Ball et al. 2000; Pandey and Brown 2000). Malaysia is not an exception to the list, as teak was reported to have been introduced into Pulau Langkawi, Kedah, from Burma in 1915 (Zakaria and Lokmal 1998), and into Sabah, Kota Marudu district, East Malaysia in 1926 by the Dutch Tobacco Company (Lapongan 2000). The increasing worldwide demand for teak wood, and the alarming decline in the currently available resources, has resulted in an intensification of teak planting activities since the early 1970s (Ball et al. 2000; Keogh 2000; Keogh 2001). Choosing the best teak origins remains a crucial requirement to maximise productivity, bearing in mind that teak timber yields and quality are prone to vary considerably depending on planting site conditions (Kaosa-ard 2000; Keogh 2001). Notwithstanding the usefulness of the scientific information that can be drawn from such studies (Kjaer et al. 1995; Madoffe and Maghembe 1988; Pedersen et al. 2007), there is still a lack of knowledge on genetic influences and heritability estimates for traits of major economic values for this species. These arguments prompted us to investigate and compare the performance of different teak origins, including clonal seed orchard (CSO) families established from seeds in 1997 at Taliwas, Sabah, East Malaysia. The corresponding findings constitute the subject matter of the current paper.

2 Materials and methods

2.1 Plant material

The plant materials were derived from 41 different origins of *T. grandis* seeds as detailed in Table 1. The

terminology used throughout this paper is in accordance with Zobel and Talbert (1984). Uncertainty remained about the genetic relatedness of seeds from seed lots 8367, 8668, and 9999, and the 26 derived from the clonal seed orchard at La Sangoué, Ivory Coast (Dupuy and Verhaegen 1993), i.e., whether they were collected from one or more trees.

The different seed lots were germinated in sand beds after subjecting the dry fruits to the usual procedure recommended for teak seeds (Tewari 1992). This consisted of alternating overnight soaking and daytime exposure to full sunlight for 7 days. A few days after sowing, young seedlings bearing at least four fully developed leaves and ranging from 2 to 4 cm in height were potted individually in 10×15 cm black plastic bags filled with local soil. They were then raised for 3 months under appropriate nursery conditions until they reached an average 15 cm stem height suitable for field planting. The sample size was determined by the number of plants per origin displaying the same vigour.

2.2 Trial characteristics, analysis criteria, and statistical processing of data

The trial was planted in March 1997 at a place called Taliwas, located at km 18 on the road from Silam to Danum Valley, Sabah, East Malaysia (Lat 4°58'N, Long 118°13'E). Monthly temperatures were 26–28°C and the mean annual rainfall (MAR) averaged 2,500 mm without a distinct dry season. The planting area was flat, 40 m above sea level, at the bottom of a valley, close to a river, and prone to short periods of flooding, which called for the creation of ditches inside and around the trial. The site, whose characteristics are detailed in Table 2, was prepared by ripping and mounding just before planting.

The 41 different plant origins were planted in a randomized complete block design (Williams and Matheson 1994), consisting of three adjacent blocks. Inside each of the three blocks, each origin was represented by an elementary plot of 15 trees planted in three rows of five individuals, each row being separated from the other by a row of buffer plants. The teak trees used as buffers throughout the trial were of similar age and vigour as the experimental material, but from a different genetic source. All the trees were initially planted at a spacing of 4 m along the row and 2 m between rows, covering a total area of 29,520 m². Manual weeding was carried out uniformly throughout the trial at least twice a year. All the buffer trees were felled after 2 years before competition appeared, thereafter increasing the distance between rows from 2 to 4 m, and halving the overall density from 1,250 trees per hectare to 625 trees per hectare.

Table 1 Background of the 41 teak seed origins that were compared in Taliwas

Seed lot No.	Origin	Genetic composition of the acquired seeds	Longitude	Latitude	Elevation (m above sea level)	Average annual rainfall (mm)	Average annual temperature (°C)
8367	Prov. India, Chandrapur Maharashtra	na	78°46'E	na	na	1,420	na
8668	Prov. Thailand Mae Huat, Lampang ^a	na	99°54'E	18°39'N	350	900	27
8823	Prov. India, Sakrebail Karnataka	Mixture of 100 progenies	75°29'E	13°48'N	600	1,000	24
8824	Prov. India, Vimoli Vir. Karnataka	Mixture of 100 progenies	74°37'E	15°11'N	600	1,500	26
8831	Prov. India, Karadibetta Karnataka	Mixture of 100 progenies	75°02'E	14°05'N	650	912	24
8832	Prov. India, Gialegundi Karnataka	Mixture of 100 progenies	75°17'E	14°05'N	700	1,000	24
8833	Prov. India, Vimoli Vir. Karnataka	Mixture of 100 progenies	74°37'E	15°11'N	600	1,500	26
8835	Prov. India, Maukal Karnataka	1 OP family	76°00'E	12°15'N	850	1,532	22
8836	Prov. India, Maukal Karnataka	1 OP family	76°00'E	12°15'N	850	1,532	22
8838	Prov. India, Maukal Karnataka	1 OP family	76°00'E	12°15'N	850	1,532	22
8839	Prov. India, Maukal Karnataka	1 OP family	76°00'E	12°15'N	850	1,532	22
8841	Prov. India, Maukal Karnataka	1 OP family	76°00'E	12°15'N	850	1,532	22
8842	Prov. India, Maukal Karnataka	1 OP family	76°00'E	12°15'N	850	1,532	22
8844	Prov. India, Maukal Karnataka	Mixture of 100 progenies	74°37'E	15°09'N	600	1,500	26
9411	CSO Prov. India Nilambur	1 OP family	76°21'E	11°21'N	49	2,565	na
9412	CSO Ss Tanzania Kihuhwi	1 OP family	38°39'E	5°12'S	260	1,880	na
9416	CSO Ss Ivory Coast Kokondekro	1 OP family	na	na	na	na	na
9417	CSO Prov. India Nilambur	1 OP family	76°21'E	11°21'N	49	2,565	na
9418	CSO Prov. India Nilambur	1 OP family	76°21'E	11°21'N	49	2,565	na
9426	CSO Ss Tanzania Mtibwa (Morogoro)	1 OP family	37°39'E	6°00'S	460	1,160	na
9429	CSO Prov. India Nellicutha	1 OP family	na	na	na	na	na
9430	CSO Prov. Thailand Mae Huat	1 OP family	99°00'E	18°06'N	350	1,300	na
9431	CSO Ss Tanzania Kihuhwi	1 OP family	38°39'E	5°12'S	280	1,860	na
9432	CSO Prov. Thailand Pong Salee	1 OP family	101°01'E	19°08'N	350	1,500	na
9434	CSO Prov. India Nellicutha	1 OP family	na	na	na	na	na
9435	CSO Prov. India Nellicutha	1 OP family	na	na	na	na	na
9437	CSO Prov. India Nilambur	1 OP family	na	na	na	na	na
9439	CSO Prov. Thailand Huoi-Nam-Oon	1 OP family	na	na	na	na	na
9440	CSO Prov. India Nellicutha	1 OP family	na	na	na	na	na
9442	CSO Prov. India Nilambur	1 OP family	na	na	na	na	na
9443	CSO Prov. India Vernoli Range	1 OP family	74°35'E	15°10'N	573	2,032	na
9445	CSO Prov. India Nellicutha	1 OP family	na	na	na	na	na
9446	CSO Prov. India Vernoli Range	1 OP family	74°35'E	15°10'N	573	2,032	na
9450	CSO Prov. India Vernoli Range	1 OP family	74°35'E	15°10'N	573	2,032	na
9452	CSO Prov. India Masale Valley	1 OP family	76°10'E	11°55'N	820	1,270	na
9454	CSO Prov. Laos Paklay	1 OP family	106°00'E	15°00'N	120	200	na
9457	CSO Prov. India Purunakote	1 OP family	84°00'E	20°00'N	133	1,200–1,500	na
9458	CSO Prov. Thailand Ban Pha Lay	1 OP family	99°59'E	18°13'N	200	1,100	na
9459	CSO Prov. India Masale Valley	1 OP family	76°10'E	11°55'N	820	1,270	na
9463	CSO Ss Ivory Coast Bamoro	1 OP family	5°07'W	7°48'N	330	1,100	na
9999	Ss PNG Ex Brown River	na	147°14'E	9°20'S	400	2,100	na

Prov provenance, in accordance with Zobel and Talbert (1984), *na* information not available, *OP* open pollinated, *CSO* clonal seed orchard Ivory Coast, *Ss* seed source, in accordance with Zobel and Talbert (1984)

^anatural stand

Table 2 Characteristics of the Taliwas planting site

Lat.	4°58'N
Long.	118°13'E
Elevation	35–45 m
Rainfall regime	2,500 mm MAR without a distinct dry season
Mean monthly temperatures	26–28°C
Soil chemical analyses *	
Na (me%)	0.23
K (me%)	0.05
Ca (me%)	9.8
Mg (me%)	7.1
Fe (%)	9.9
Mn (%)	0.44
P Total (ppm)	91.5
P Available (ppm)	2.1
Al (me%)	0.02
Org C (%)	0.86
N (%)	0.11
C/N	8.8
pH H ₂ O (range of variation)	6.0–6.3
CEC	16.9
Soil texture ^a	
Clay (%)	33
Silt (%)	19
Fine sand (%)	32
Coarse sand (%)	16
Soil colour	Greyish
Soil classification	Fluvisols

^a Average values corresponding to 8 soil samples taken at a depth of 0 and 60 cm and from four different locations representing the whole planted area

2.3 Analysis criteria and statistical processing of data

The quantitative data consisted of:

1. Mortality rate “M”, established by counting the dead trees out of the total number of trees initially planted.
2. Total tree height “H” measured with a graduated pole, then with a clinometer when trees became too tall.
3. Diameter at breast height, or “DBH”, measured with a tape at about 1.3 m from the ground.

All these data were recorded for each tree 15, 25, and 104 months after planting.

The mean annual increment in height and in diameter at breast height were deduced from these measurements.

Qualitative data were also obtained for the analyses, assigning scores to the following criteria:

4. Straightness: score of 1 for straight trees, 2 for slightly crooked trees, and 3 for very crooked trees.

5. Forking: score of 1 for trees without any fork, 2 when forked in the upper half of the tree, and 3 when forked in the lower half of the tree.
6. Branching: score of 1 for few lateral and small diameter branches, 2 for medium sized branches, and 3 for a higher frequency of thicker branches.
7. Bending: score of 1 for vertical stems, 2 for stems diverging from 0 to 10° from the vertical, and 3 for wider angles of stem divergence from the vertical.
8. Fluting: score of 1 for an absence of flutes, 2 for slightly fluted, and 3 for more pronounced flutes.
9. Flowering: score of 1 for absence of flowering, and 2 when bearing flowers or fruits.

In order to minimize bias, these qualitative scores were assigned by one assessor. The statistical analyses were performed using the SAS statistical package, version 9.1 (SAS Institute Inc. 2004), PROC CATMOD and PROC GLM, and more specifically, the SAS CORR procedure for age–age and trait–trait phenotypic correlations. The various traits were analysed using a mixed model, with replicates (three) as a fixed effect and seed “origin × replicate” interaction and the family as random effects.

The general statistical mixed model applied was:

$$Y_{ijk} = \mu + R_i + O_j + (RO)_{ij} + \epsilon_{ijk}$$

Where

- Y_{ijk} Observation on the k th individual of the j th seed origin in the i th replicate
- μ Overall mean
- R_i Fixed effect of the “replicate” factor, $1 \leq i \leq 3$
- O_j Random effect of the “seed origin” factor, $1 \leq j \leq 41$
- $(RO)_{ij}$ Random effect of the interaction between “replicate” and “origin”
- ϵ_{ijk} Residual error

Individual tree heritabilities were calculated for the CSO families only (26 families from 42 seed lots), for which we assumed strict half-sib families using the following formula:

$$h^2 = \frac{4\hat{\sigma}_O^2}{\hat{\sigma}_O^2 + \hat{\sigma}_{R^*O}^2 + \hat{\sigma}_e^2}$$

Where:

- $\hat{\sigma}_O^2$ is the “origin” variance component
- $\hat{\sigma}_{R^*O}^2$ is the “origin × replicate” interaction variance component
- $\hat{\sigma}_e^2$ is the residual error

The variance components for growth traits were estimated using the restricted maximum likelihood method of the SAS VARCOMP procedure (SAS Institute Inc. 2004). The

Table 4 Significance levels (*p* values) of the two “Replicate” and “Seed Origin” experimental factors tested and of their interaction (R × O) on the nine traits observed at different dates after planting at Taliwas

Time (months)	Factors	Traits								
		Mortality	Height	DBH	Straightness	Forking	Branching	Bending	Fluting	Flowering
15	Replicate (R)	<0.05	<0.0001	<0.0001	na	na	na	na	na	na
	Origin (O)	NS	<0.0001	<0.0001	na	na	na	na	na	na
	R × O	NS	0.0001	<0.05	na	na	na	na	na	na
25	Replicate (R)	NS	NS	<0.0001	<0.0001	<0.0001	<0.0001	NS	na	na
	Origin (O)	<0.01	<0.0001	<0.0001	<0.0001	<0.05	<0.0001	<0.0001	na	na
	R × O	NS	<0.0001	NS	<0.0001	<0.001	<0.0001	<0.05	na	na
104	Replicate (R)	<0.05	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.001	NS	NS
	Origin (O)	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	R × O	NS	<0.0001	NS	<0.0001	<0.05	<0.0001	<0.0001	<0.0001	<0.0001

and the highest values of 5.6 m/year and 5.4 cm/year, respectively, for family 9443; these notably diminished later (Table 5).

The fact that the final values for height in particular, and also for DBH, could barely be predicted from the first assessments made at 15 and 25 months, in that taller trees did not necessarily have a larger DBH, except for CSO family 9430, was consistent with the respective correlation coefficient values summarized in Table 6.

Narrow sense heritabilities for height and DBH increased gradually as the trees aged from 0.35 to 0.76 and from 0.41 to 0.46 for height and DBH, respectively, reaching relatively high values, especially for height at 104 months (Table 7).

The 41 origins assessed had a significant effect on the six qualitative criteria observed 25 and 104 months after planting, notwithstanding replicates and “replicate × origin” interaction effects (Table 4). The corresponding data are detailed in Table 8. Overall, trees from the CSO families were less crooked and grew more vertically than those from the native

provenances (Table 8, Fig. 2). This was particularly obvious for families 9417, 9426, 9437, and 9463, with 100% of straight trees, and families 9418, 9435, and 9439 with 98% of straight trees 104 months after planting. In contrast, most of the India Karnataka, Maukal lots, with a special mention for 8835, 8836, and 8838, were characterized by a strong inclination to bending. The distinction between the CSO families and the other origins was less evident for forking, branching, and fluting (Table 8, Fig. 2). The largest proportion of forkless trees (32%) was observed for seed lot 8367 (Provenance India, Maharashtra, Chandrapur), followed by the two CSO families 9429 (India Nelicutha) and 9443 (India Vernoli Range) with 20% and 19% of forkless trees, respectively. CSO family 9429 (India Nelicutha) and seed lot 8367 (Provenance India, Maharashtra, Chandrapur) were also characterized by trees with reduced branching (36% and 32% as respective proportions). Another asset of CSO families 9429, 9430, and 9417 was that they were less affected by fluting than the other origins after 104 months, with 86%, 83%, and 82% of fluteless trees,

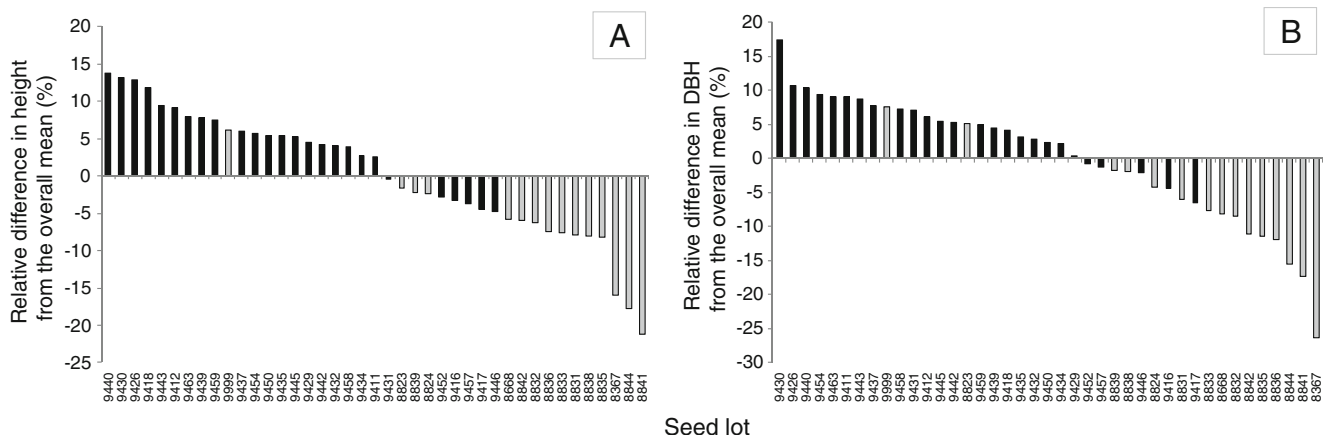
**Fig. 1** Relative differences in mean height (a) and in mean DBH (b) for each of the 41 origins—CSO in *dark*—with the overall average expressed as zero at 104 months

Table 8 Number of trees recorded (N), relevant mortality (M) and mean values 104 months after planting for the six qualitative traits assessed on the 41 teak origins—CSO in grey cells—planted at Taliwas

Seed lot No.	N	M %	Straightness			Forking			Branching			Bending			Fluting			Flowering						
			Mean	C1	C2	C3	Mean	C1	C2	C3	Mean	C1	C2	C3	Mean	C1	C2	C3	Mean	NF*				
8367	37	18	1.1	92	8	0	2.1	32	27	41	2.0	32	32	36	1.4	68	30	2	1.4	59	38	3	1.1	95
8668	44	2	1.1	91	9	0	2.6	9	23	68	2.3	9	52	39	1.1	89	11	0	1.7	39	50	11	1.1	89
8823	39	13	1.1	92	8	0	2.3	18	33	49	2.0	18	64	18	1.4	67	31	2	1.3	77	21	2	1.0	100
8824	39	13	1.2	85	15	0	2.6	5	31	64	2.5	3	49	48	1.4	64	28	8	1.5	54	38	8	1.1	92
8831	36	20	1.1	94	6	0	2.6	6	31	63	2.5	8	36	56	1.2	78	22	0	1.3	69	28	3	1.0	100
8832	37	18	1.1	86	14	0	2.8	0	19	81	2.6	0	43	57	1.2	84	14	2	1.6	51	41	8	1.0	97
8833	43	4	1.1	88	12	0	2.4	19	23	58	2.2	16	47	37	1.4	65	28	7	1.4	60	37	3	1.1	93
8835	35	22	1.4	63	37	0	2.7	3	26	71	2.5	0	51	49	1.7	49	34	17	1.8	31	54	15	1.0	100
8836	33	27	1.3	70	30	0	2.8	3	12	85	2.6	0	42	58	1.6	52	39	9	1.6	45	48	7	1.1	91
8838	42	7	1.1	86	14	0	2.4	12	36	52	2.3	7	57	36	1.6	52	36	12	1.6	50	36	14	1.0	98
8839	39	13	1.2	79	21	0	2.6	5	26	69	2.5	3	44	53	1.4	72	15	13	1.2	82	15	3	1.0	100
8841	32	29	1.1	91	6	3	2.8	0	22	78	2.7	3	22	75	1.4	75	13	12	1.4	63	37	0	1.0	100
8842	34	24	1.1	97	0	3	2.4	6	50	44	2.3	12	50	38	1.2	82	12	6	1.3	74	26	0	1.0	100
8844	40	11	1.1	90	10	0	2.8	5	10	85	2.4	8	42	50	1.2	85	13	2	1.4	65	30	5	1.1	88
9411	38	16	1.0	97	3	0	2.9	0	11	89	2.6	3	39	58	1.1	92	8	0	1.4	66	26	8	1.1	95
9412	37	18	1.1	95	5	0	2.6	8	27	65	2.4	8	41	51	1.1	89	8	3	1.8	30	62	8	1.2	84
9416	40	11	1.0	98	2	0	2.4	15	30	55	2.4	13	40	47	1.2	88	8	4	1.6	45	50	5	1.2	83
9417	33	27	1.0	100	0	0	2.7	3	24	73	2.2	18	43	39	1.0	97	3	0	1.2	82	15	3	1.0	97
9418	44	2	1.1	93	7	0	2.5	7	34	59	2.3	0	68	32	1.0	98	2	0	1.3	77	18	5	1.0	95
9426	41	9	1.0	100	0	0	2.8	2	15	83	2.3	0	73	27	1.1	93	7	0	1.7	37	54	9	1.1	85
9429	44	2	1.1	91	9	0	2.3	20	30	50	1.8	36	43	21	1.1	93	7	0	1.1	86	14	0	1.0	95
9430	35	22	1.1	94	6	0	2.3	17	37	46	2.1	11	63	26	1.1	97	0	3	1.2	83	17	0	1.1	94
9431	37	18	1.2	81	19	0	2.5	14	24	62	2.4	16	24	60	1.3	78	16	6	1.9	19	76	5	1.1	86
9432	41	9	1.1	90	10	0	2.8	5	15	80	2.3	2	68	30	1.3	71	27	2	1.9	27	54	19	1.1	90
9434	41	9	1.1	85	15	0	2.8	2	17	81	2.5	2	41	57	1.1	88	10	2	1.3	76	20	4	1.1	88
9435	43	4	1.0	95	5	0	2.6	12	21	67	2.1	16	53	31	1.0	98	2	0	1.3	74	26	0	1.0	95
9437	40	11	1.0	100	0	0	2.4	15	33	52	2.2	15	50	35	1.1	95	3	2	1.3	70	30	0	1.1	88
9439	41	9	1.0	98	2	0	2.3	10	46	44	2.2	10	61	29	1.0	98	2	0	1.4	61	39	0	1.1	90
9440	41	9	1.0	95	5	0	2.8	2	17	81	2.5	0	54	46	1.1	85	15	0	1.5	51	49	0	1.0	95
9442	42	7	1.1	93	7	0	2.4	12	36	52	2.3	12	43	45	1.1	88	12	0	1.5	55	40	5	1.1	86
9443	44	2	1.1	93	7	0	2.4	19	23	58	2.0	23	52	25	1.1	86	14	0	1.7	39	50	11	1.1	86
9445	42	7	1.0	95	5	0	2.4	14	31	55	2.2	12	52	36	1.1	90	5	5	1.5	55	43	2	1.1	90
9446	35	22	1.1	91	9	0	2.9	3	0	97	2.4	14	29	57	1.2	86	9	5	1.6	46	49	5	1.3	74
9450	42	7	1.0	98	2	0	2.7	2	29	69	2.5	0	52	48	1.0	95	5	0	1.4	64	36	0	1.0	95
9452	42	7	1.1	88	12	0	2.9	0	10	90	2.6	0	38	62	1.4	76	12	12	2.0	29	45	26	1.5	55
9454	33	27	1.1	91	9	0	2.7	6	21	73	2.4	12	39	49	1.3	82	9	9	1.5	48	48	2	1.1	88
9457	33	27	1.0	97	3	0	2.7	6	21	73	2.3	12	48	40	1.1	91	9	0	1.4	61	36	3	1.2	82
9458	39	13	1.1	90	10	0	2.7	0	28	72	2.5	3	44	53	1.3	74	21	5	1.8	38	46	16	1.2	79
9459	40	11	1.3	72	28	0	2.6	8	22	70	2.4	5	50	45	1.3	80	15	5	2.0	25	55	20	1.4	63
9463	43	4	1.0	100	0	0	2.9	0	9	91	2.6	0	40	60	1.0	95	5	0	1.9	23	60	17	1.1	93
9999	43	4	1.0	95	5	0	2.7	5	16	79	2.1	5	77	18	1.1	88	9	3	1.6	42	53	5	1.6	42
Mean	39	13	1.1	91	9	0	2.6	8	24	68	2.3	9	48	43	1.2	82	14	4	1.5	54	39	7	1.1	89

This includes the distribution ratios (as a%) in the different classes C1, C2 and C3 established by scoring the five qualitative criteria (see text) except for flowering (*:% of non flowering trees)

characteristics, may account for the good survival rate and much higher height and DBH values than in other locations (Bekker et al. 2004; Kadambi 1972; Madoffe and Maghembe 1988). The MAR and duration of the dry season are increasingly being acknowledged as having a determining influence on teak growth (Keiding et al. 1986; Keogh 1979). This observation should encourage the planting of suitable teak germplasm under wet conditions, keeping in mind that natural teak provenances include sites with high rainfall (>2,500 mm/year; Keiding et al. 1986). In this respect, our study provides useful information on teak survival, on growth, and on the qualitative traits studied, under high rainfall conditions, at least up to about 9 years after planting. The marked reduction in Mean Annual Increment (MAI) found for growth after 25 months, from 4.7 to 1 m for height and from 4.7 to 1.2 cm for DBH, may have been partly due to increased tree-to-tree competition, despite a drastic reduction in the initial density from 1,250 to 625 trees per hectare 24 months after planting, by thinning all the buffer trees. The high water table at the site also probably limited the depth of root system penetration and may also have contributed to this marked decline in H and DBH growth. At Longuza (Tanzania), a much higher

growth rate was also found in the first few years, with a MAI of 2.3 to 2.7 m at 5 years as opposed to 1.3 to 1.6 m at 17 years (Madoffe and Maghembe 1988). Another hypothesis is that, after reaching a certain development in height and diameter, teak allocates a greater share of its metabolism to heartwood formation to the detriment of growth in these dimensions. However, this does not seem to be the case as several observations at the same Taliwas site (Goh et al. 2007; Goh and Monteuis 2009) have indicated that the heartwood formation process actually starts very early, without any detrimental effects on height and diameter increments. This observation was also reported by Bath (2000). Such early heartwood formation constitutes another reason to plant fast-growing teak trees to be harvested at shorter rotations (Chaix et al. 2008; Goh and Monteuis 2005).

Our results showed that teak growth and qualitative traits are strongly influenced by provenance (broad sense) effects and, in this respect, our observations were consistent with those of several others (Kaosa-ard 2000; Keiding et al. 1986; Madoffe and Maghembe 1988). The fact that the CSO families grew faster and were of better quality overall, with less between-tree variation than the other provenance

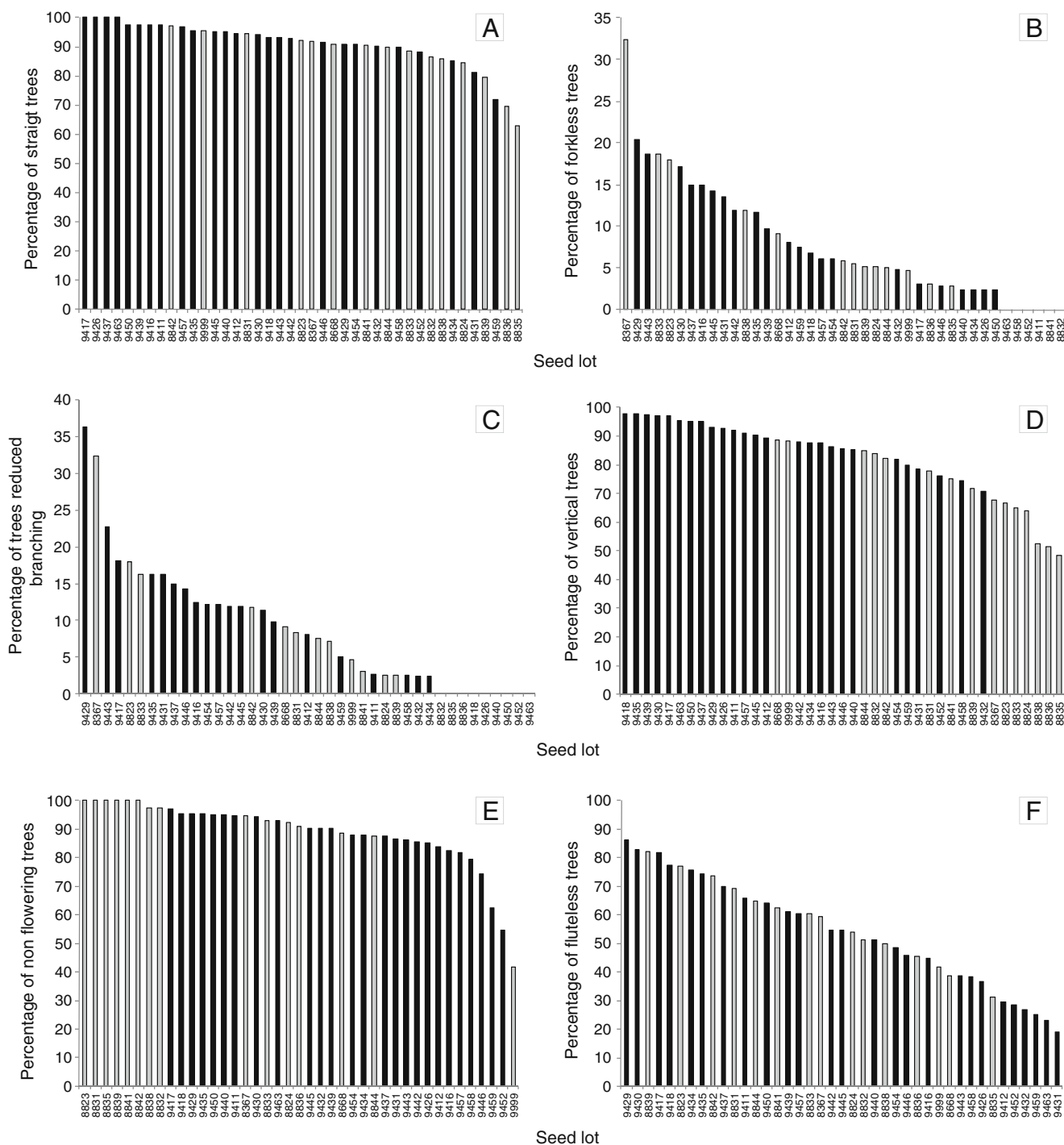


Fig. 2 Proportions (%) of: **a** straight trees (scored 1 for straightness), **b** trees without any fork (scored 1 for forking), **c** trees with reduced lateral branching (scored 1 for branching), **d** vertical trees (scored 1

for bending), **e** trees without any flowers (scored 1 for flowering), **f** fluteless trees (scored 1 for fluting) for each origin—CSO in *dark*—assessed 104 months after planting

origins, may have been due to several factors. First of all, these families were derived from superior trees and were each produced by only one mother genotype (Dupuy and Verhaegen 1993), whereas greater uncertainty remained regarding the selection and the number of seed producers

from which the provenance and seed source seed lots came. Secondly, the clonal seed orchard at La Sangoué was set up to improve the overall genetic quality of seeds resulting from the intercrossing of superior phenotypes from quite different provenances. Those were soundly selected and

Table 9 Correlation coefficients for height (H), DBH, straightness (STR), forking (F), bending (B), branching (BR), flowering (FLO) and fluting (FLU) established 25 and 104 months after planting for the 41 teak origins as a whole

Criteria	After 25 months				After 104 months					
	STR	F	B	BR	STR	F	B	FLO	FLU	BR
H	-0.39	-0.24	-0.48	NS	-0.16	NS	-0.33	0.08	0.08	-0.12
DBH	-0.20	NS	-0.23	0.14	-0.13	0.11	-0.20	0.15	0.18	NS
STR		0.34	0.52	NS		0.09	0.47	NS	0.09	0.15
F			0.15	NS			0.13	0.06	0.15	0.60
B				NS				-0.05	0.08	0.22
FLO				Na					0.13	NS
FLU				Na						0.17*

Na not available, NS values not indicated as not statistically significant ($p > 0.05$)

*significant at $0.001 < p \leq 0.05$; other values are statistically significant at $p \leq 0.001$

wisely located within the orchard to favour outcrossing and the capturing of both additive and heterosis genetic effects (Dupuy and Verhaegen 1993), unlike under native stand conditions. The fertilization regime in teak is largely allogamous with high outcrossing rates (Kadambi 1972), as confirmed by genetic marker studies (Indira et al. 2008; Kertadikara and Prat 1995; Kjaer and Suangtho 1995). Hence, different genetic environments and gene flows, depending on the respective physical locations of the grafted genotypes flowering at the same time within the orchard, may have been responsible for the noticeable performance variations found between families derived originally from the same native provenance (CSO families 9446 and 9443 for instance). The conditions, and particularly the climatic characteristics of the sites at which the seeds were produced, can be logically assumed also to play a noticeable role. Between-genotype differences in flowering capacity or synchronism may induce site-related preferential mating systems. Specific combining abilities have also been assumed to play a key role in the genetic quality of seeds produced from CSOs (White et al. 2007; Zobel and Talbert 1984). Some or all of these factors may have been responsible for the better performance of the CSO families compared to the seed lots collected directly from the same original provenances. The comparison between CSO family 9430 and seed lot 8668 from the same native provenance of Mae Huat, Lampang, Thailand, provides a striking example of the great benefit of including a CSO phase in a teak tree improvement and selection programme. Seed source 9999 (Papua New Guinea ex Brown River), assumed to be of seed orchard origin, gave similar mean height and DBH values to those of the CSO families.

For rigour and accuracy reasons, the heritability estimation was limited to the height and DBH quantitative traits of the CSO families, each being the only ones derived from a

single mother genotype. The corresponding values found for height and DBH were higher than those reported in the literature (Callister and Collins 2007; Danarto and Hardiyanto 2001). In spite of the fact that the heritability estimation could have been inflated by the single site and by not having strict half-sib families, this suggests that height in teak could be usefully controlled by additive gene actions, contrary to the assumption of Gogate et al. (1997). The slight increment in height and DBH heritability values with age observed here, and for different species (White et al. 2007), might have been due a reduction in environmental variation, which may have been associated with canopy closure and competition for light.

The rationale for estimating genetic correlations between economically important traits, which are currently insufficiently known for teak, to provide information on trait-to-trait relationships and for use in tree selection, has already been stressed (Callister and Collins 2007). However, the weakness of the correlation coefficient values obtained failed to provide useful information in this respect, except between straightness and bending, and forking and branching, all of which have major impacts on timber value and the use of teak logs (Baillères and Durand 2000; Ladrach 2009). This is why these traits have been taken into consideration in most teak genetic improvement analyses (Kaosa-ard 1999; Keiding et al. 1986; Kjaer and Lauridsen 1996). The huge benefits of growing teak with reduced lateral branching or natural self-pruning, thereby avoiding the costly and labour-intensive pruning operations practised in a lot of teak plantations to reduce knot and node formations, have to be kept in mind (Bekker et al. 2004; Ladrach 2009).

The first flowering in teak is considered to be an important factor in determining clear bole length, hence tree value. It is initiated in terminal stem buds in almost all trees. The conversion of those buds from the vegetative to

the reproductive stage disrupts their capacity to ensure bole elongation, while also inducing the formation of two opposite branches, or a fork, as a result of a true dichotomy process. This explains why forking is usually highly and positively correlated with flowering in teak a few years after the first flowers have appeared (Dupuy and Verhaegen 1993; Kaosa-ard 1999). The late onset of flowering in most teak origins in the Taliwas trial, compared to other sites (White 1991) and particularly in Ivory Coast (Dupuy and Verhaegen 1993), where the ortets of the CSO clones were selected, for their delayed flowering among other things, suggests a site effect for flowering onset, as already suggested (Kadambi 1972). The very low correlation (0.08) between height and flowering in our study might have been because only a few trees had entered the flowering stage, and only recently, giving rise to observable forks. There are different types of forks in teak (Kadambi 1972). Most of those recorded in our study differed from flowering-induced forks by the persistence of the main stem which, in the absence of flowering, continued to elongate to reach the great heights recorded. The whorls of large branches at those forks may account for the high positive correlation values found between forking and lateral branching. The surprisingly high proportion of forked trees characterizing the whole trial may be due to the influence of external factors, such as floods or root contact with a high water table, which may have inhibited natural apical dominance, thereby stimulating axillary shoot formation. The fact that most of the forks appeared in the lower half of the trees (Table 8), forming a few years after planting and concomitantly with a growth rate reduction, supports this assumption.

5 Conclusions

This study provided useful information on the behaviour of different genetic origins of teak seedling trees as regards the expression of major economic traits. The wet conditions at the site seemed to have a strong positive effect on overall growth performance and also on bole quality. In general, the CSO families traced to selected superior ortets in Ivory Coast, exhibited superiority under the different conditions at Taliwas. This demonstrates the usefulness of CSOs for the genetic improvement of teak, in spite of a few handicaps (Katwal 2008; Kjaer and Foster 1996; Kjaer et al. 2000), and shows that selection in one environment can have positive carry-over effects in another, even when located on a different continent with different climatic and edaphic conditions.

Consistently with other studies (Kjaer et al. 2000), the substantial variation observed between and within the seedling families, even from the same ultimate origins,

encourages the use of clones under such favourable wet conditions in order to maximise the early substantial returns in yield and quality of teak plantations. This trial offers huge opportunities for selecting and testing superior genotypes for clonal mass propagation and wise deployment, and also for use as breeding populations for advanced generations of genetic improvement (Goh and Monteuis 2005).

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