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.

Olivier Monteuuis[1], Doreen K S Goh [2], Charles Garcia[3], David Alloysius[4], Jikos Gidiman[4], Roberto Bacilieri[5], Gilles Chaix [6]

[1]CIRAD - BIOS Department - UMR AGAP, TA A-108/03- Avenue Agropolis, F-34398 Montpellier, Cedex 5 France.

[2] YSG Biotech Sdn Bhd, Yayasan Sabah Group, Voluntary Association Complex, Mile 2 ½, off Tuaran Road, P. O. Box 11623, 88817 Kota Kinabalu, Sabah, Malaysia

[3] Forestry Division, Yayasan Sabah Group, Rakyat Berjaya sdn Bhd, 2nd,4th,5th & 6th Floor, UMNO Building, P.O. Box 60793, 91017 Tawau, Sabah, Malaysia

[4] Conservation and Environmental Management Division, Yayasan Sabah Group, Rakyat Berjaya sdn Bhd, 5th & 6th Floor, UMNO Building, P. O. Box 60793, 91017 Tawau, Sabah, Malaysia

[5]INRA-CIRAD-SUPAGRO, UMR AGAP 1334, Genetic Improvement and Adaptation of Mediterranean and Tropical Plants, 2 pl. Viala, F-34060 Montpellier, France

[6] CIRAD - BIOS Department - UMR AGAP, TA A-108/16 - 73 rue Jean-François Breton, F-34398 Montpellier, Cedex 5, France.

Abstract

Forty-two different genetic origins of teak (*Tectona grandis*) comprising 26 open-pollinated (OP) families from a clonal seed orchard (CSO) were planted in a replicated trial under 2,500mm of annual rainfall and no distinct dry season, in 1997, in Sabah, East Malaysia. The trees were measured or scored for various traits at 13, 35, 49, 61, 72, 85, 96 and 106 months after planting. Mortality rate, height "H", diameter at breast height "DBH", volume "V" and fork height "FH" varied strongly among populations and origins. The best population means after 106 months for growth H (21.1m), DBH (21.1cm) and V (278dm^3), were for the CSO families. Narrow sense heritabilities for the CSO families increased gradually with age but remained lower after 106 months for DBH (h^2 = 0.24) and V (h^2 = 0.34) than for H (h^2 = 0.51) and FH (h^2 = 0.56). Overall, the CSO families were also straighter, less forked and grew more vertically than the native provenance and seed-derived sources. Such differences did not exist for flowering ability, and at 106 months the great majority of the trees of the various origins had not yet entered the flowering stage. Overall, at 106 months, the phenotypic correlations between the various quantitative and qualitative traits were weak, except between straightness and bending with values higher than 0.50. These findings confirm the usefulness of CSO for teak improvement and demonstrate the beneficial influence of wet tropical conditions on traits of major economical importance for this species.

Key words: CSO . Genetic improvement . Growth rate . Heritability . Qualitative traits . Provenance . Seed source.

Introduction

Tectona grandis Linn. f., commonly known as teak, belongs to the *Verbenaceae* family. The species occurs naturally in India, Laos, Myanmar (ex-Burma) and Thailand, mostly under mean annual rainfall ("MAR") of 1,000 to 1,500 mm with a distinct dry season (White 1991; Tewari 1992). Some provenances however can thrive under much higher precipitations (Keiding et al 1986). Teak has been recognized for centuries as one of the most prized high value timbers due to outstanding wood properties, with special mention for durability and aesthetic features (Kadambi 1972; Pandey and Brown 2000; Keogh 2001). Its wood is suitable for a wide range of end-uses, either as sawn-timber or veneer, from furniture making to shipbuilding (Tewari 1992; Bath 2000). This popularity has accounted for extensive establishment of plantations within and beyond its native range (Ball et al 2000; Pandey and Brown 2000), starting with Indonesia where it was introduced some 400-600 years ago and is now considered as sub-spontaneous (Kaosa-ard 2000; Siswamartana 2000). Since the early 1970's, the increasing worldwide demand for teak wood on one hand and the alarming diminution of the resources currently available on the other has resulted in a noticeable escalation of teak planting to produce in the shortest possible delays large quantities of superior quality teak timber (Ball et al. 2000; Keogh 2000, 2001). Selecting planting materials best adapted to plantation sites is a prime requisite for the success of such a venture. This requires knowledge of genetic origin effects and of origin X site interactions, leading to ultimate timber yield and quality (Keiding et al. 1986; Kaosa-ard 2000; Keogh 2001). Such information as well as genetic influences and heritability estimates for traits of major economical values remains so far limited in teak (Madoffe and Maghembe 1988; Kjaer et al. 1996; Murillo and Badilla 2004; Pedersen et al. 2007). Most of these studies referred to sites with a distinct dry season and mean annual rainfall ("MAR") ranging between 1,200 and 1,500mm. However, it can be logically assumed for teak like for many other timber species that wetter conditions may result in earlier and higher yields while preserving the quality required (Keiding et al., 1986; Keogh 1979).

These arguments prompted us to study the influence of humid tropical conditions of Sabah, East Malaysia, on diverse teak origins, including clonal seed orchard (CSO) families. The analysis was done with regard to quantitative and qualitative criteria (Keiding et al 1986). The quantitative criteria included mortality, tree and fork height, diameter and volume that determine yield. The qualitative criteria for economical value of bole consisted of straightness, forkiness, bending and flowering. In teak, flowering induces fork formation whereby the earlier it flowers, the shorter the clear bole length and hence, the lesser its market value (White 1991; Monteuuis et al 1995).

Materials and methods

Plant material

The plant material derived from 42 different origins of *Tectona grandis* seeds, with respective characteristics,detailed in Table 1. The terminology used throughout this paper is in accordance with Zobel and Talbert (1984): the natural stands are referred to as provenances ("Prov") and planted stands as seed sources ("Ss"). Information on the CSO of La Sangoué, Ivory Coast is given in Dupuy and Verhaegen (1993). However, for most of these origins, the 26 CSO open families included, uncertainty remains on the genetic relatedness of the seeds, i.e. whether they have been collected from one or several trees.

The different seed lots were germinated in sand bed after having applied to the dry fruits the usual procedure recommended for teak (Tewari 1992). This consisted in alternating overnight soaking and day long exposure to full sun for seven days. A few days after sowing, the young seedlings with at least 4 fully developed leaves and 2 to 4 cm in height were potted individually in 10 x 15 cm black plastic bag containers filled with clayish local top soil. The seedlings were then raised for 3 months in suitable nursery conditions until they reached an homogenous average stem height of 15 cm for field planting. Sampling size was determined by the availability of plants with the same vigor per origin.

Trial characteristics

The trial was set up in May 1997 in compartment 311 of the Luasong Forestry Center located at 120km west from Tawau, Sabah, East Malaysia (Lat 4° 35' N, Long117° 40' E). Monthly temperatures were 26-28°C and MAR averaged 2,500mm without a distinct dry season The planting site situated at 130-170m above sea level was rather hilly, along a slope of about 15° gradient with characteristics detailed in Table 2. It was prepared by ripping and mounding just before planting.

The 42 different origins of plants were established according to a randomized complete block design (Williams and Matheson 1994), consisting of 3 contiguous blocks taking into account the variation of topography. Within each of these 3 blocks, each origin was represented by an elementary plot of 15 trees from the same seed lot. These trees were planted in 3 rows of 5 individuals, each row being separated from the other by a row of buffer plants also used to fill the ravines. The teak trees used as buffer 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 4m along the same line and 2 m between lines, covering a total surface of 45 x 42 x 2 x 4 x2 = 30,240m^2. All the buffer trees were felled after 2 years, increasing from that time onwards the between line distance from 2m to 4m, and halving the overall density from 1,250 trees/ha to 625/ha.

Analysis criteria and statistical treatment of the data

The quantitative data consisted of:

1. mortality rate "M", established by counting the dead trees out of the total number of tree initially planted.

2. total tree height "H" (in m) measured with a graduated pole, then with a clinometer when trees became too tall.
3. diameter at breast height or "DBH" (in cm) measured with a tape at about 1.30 m above soil level.
4. stem fork height "FH" (in m), recorded for forked trees.
5. bole volume "V" (in dm^3), calculated by using the following formula:

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

All these data were recorded or established for each origin 13, 35, 49, 61, 72, 85, 96 and 106 months after planting, except for FH measured only at 106 months.

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

6. straightness: score 1 for the straight trees, 2 for slightly crooked ones and 3 for the trees very crooked.
7. forkiness: score 1 for trees without any fork, 2 when forked in the upper half of the trees and 3 when below.
8. Bending: score 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.
9. Flowering: score 1 in absence of flower, 2 when bearing flowers or fruits.

In order to minimize bias, these qualitative scores were assigned by a single and same assessor.

The statistical analyses were performed using SAS statistical package, Version 9.2 (SAS Institute Inc., 2008). Proc GLM was used for the analyses of variances with block replicates, seed origin and seed origin X replicate interaction. The linear statistical 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 : Effect of the factor “replicate”, $1 \le i \le 3$;

O_j :: Effect of the factor seed “origin”, $1 \le j \le 42$;

$(RO)_{ij}$: Effect of the interaction between “replicate “ and “origin”;

ϵ_{ijk} : Residual error.

PROC CATMOD was used for analyzing the qualitative traits data, assigning 1 to score 1 and 0 to scores 2 and 3, whereas PROC REG was applied to age-age and trait-trait phenotypic correlations for the 42 origins assessed.

Individual tree heritability estimates, with relevant standard errors established according to Falconer and Mackey (1996), were calculated only for the CSO families, assuming these consisted of half-sibs exclusively, and 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 family variance component;

$\hat{\sigma}_{R*O}^2$ is the variance component of family x replicate interaction;

$\hat{\sigma}_e^2$ is the residual error.

Relevant variance components limited to growth traits were calculated using the restricted maximum likelihood (REML) method of the SAS VARCOMP procedure (SAS Institute Inc. 2008), with “replicate” as fixed effect factor, and “family”, and “family x replicate” as random effect factors. The linear statistical model applied was:

$Y_{ijk} = \mu + R_i + F_j + (RF)_{ij} + \epsilon_{ijk}$

where

Y_{ijk} : Observation on the k^{th} individual of the j^{th} family in the i^{th} replicate;

μ : Overall mean;

R_i : Fixed effect of the factor “replicate”, $1 \leq i \leq 3$;

F_j : Random effect of the factor “family”, $1 \leq j \leq 26$;

$(RF)_{ij}$: Random effect of the interaction between “replicate “ and “family”;

ϵ_{ijk} : Residual error.

Results

Mortality losses varied more or less among block replicates and plant origins during the course of time (Table 3). At 106 months after planting, 84 % of the trees initially planted were still alive. Seed lots 9424 (CSO Ss Tanzania Mtibwa), 4314 (Solomon Islands Arara) and 9450 (CSO Ivory Coast, Prov. India Vernoli range) were the less affected by mortality with 96% to 100% survival rates (Table 4). The highest mortality rates of 33% and 40% were recorded for seed lots 9436 (CSO Prov. India Nellicutha) and 8839 (Prov. India Maukal Kamataka, open-pollinated family) respectively. Mortality between origins varied up to 35 months and diminished noticeably later on, with higher risks of predictions between 13 and 106 months ($0.48 \leq R \leq 0.53$, $P < 0.0001$) than between 35 and 106 months ($0.86 \leq R \leq 0.91$, $P < 0.0001$). Height “H”, “DBH” and volume “V” were strongly influenced by the factors “replicate”, “origin” and their interaction from 13 to 106 months after planting, and likewise for fork height “FH” after 106 months (Table 3). From 13 months till the end of the observation period, the mortality-free seed lot 9450 (CSO Ivory Coast, Prov. India Vernoli range) produced the taller trees, with a mean H of 21.1m, whereas seed lot 9449 (CSO Ivory Coast, Prov. Thailand Pong Salee) gave rise to the bigger ones, with a mean H of 21.1m, DBH of 21.1cm and bole volume of 278 dm^3 after 106 months (Table 4 and Fig. 1a, 1b and 1c). The between-tree variation was also weaker for these two lots than for the other origins. For the same criteria, only seed lots 8669 (Prov. Thailand Mae Huat Lampang, planted stand) and 8367 (Prov. India Chandrapur Maharastra) appeared much inferior to the others since the beginning. Height, DBH, volume and fork height averages varied greatly ($P < 0.0001$) for each assessment date among seeds coming from natural stands (Prov), from planted stands (Ss) and also from the CSO. Between 13 to 106 months after planting, natural stand origins gave rise to the lower averages for these four criteria, while the higher scores were recorded for the CSO families with individuals of more than 28m in H (families 9418, 9437, 9450, 9463), 33cm in DBH (families 9426 and 9449), and 760 dm^3 in bole volume (CSO families 9449, 9426 and 9463) at 106 months (Table 4). Solomon Islands seed sources 5212 and 4314 performed similarly to CSO families for the same four quantitative traits and more particularly for DBH and volume (Table 4, Fig. 1b and 1c).

At 106 months after planting, mean annual increments averaged 1.9 m for H, 2 cm for DBH and 20.3 dm^3 for volume with the best performances for the CSO families 9412, 9449, 9450 and seed lot 5212 (more than 2.2 m, 2.2 cm and 29 dm^3), whereas the lowest mean values (1.2 m, 1.3 cm and 5.7 dm^3) were recorded for seed lot 8367 Overall, H and DBH annual growth rates were higher during the first 49 months than between 49 and 106 months (2.7 m/yr vs 1.3 m/yr and 2.9 cm/yr vs 1.2 cm/yr as respective mean values, Fig. 1a and 1b). Bole volume, in contrast, increased faster after 49 months than earlier on (Fig. 1c), with much reduced within origin variation. The fact that final measurements for height, except for lots 9450 and 8367 (Fig. 1a), could hardly be predicted from the assessments made before 49 months is consistent with the small coefficient of correlation values found for the relevant periods. However, improvement could be observed 49 months after planting (Table 5). DBH appeared to be more predictable earlier, with correlation coefficient values of more than 0.85 starting from 49 months after planting (Table 5 and Fig. 1b). This seemed to be even more obvious for bole volume (Fig. 1c). The correlation coefficient values were not high enough to establish a clear relationship between H, DBH and fork height recorded after 106 months (Table 5), despite obvious ranking similarities for these three traits and also for bole volume (Table 4).

Narrow sense heritabilities for height, DBH and volume increased gradually as the trees aged, but remained overall low at 106 months, especially for DBH ($h^2 = 0.24$) and volume ($h^2 = 0.34$). Heritability values obtained at the same time for height ($h^2 = 0.51$) and fork height ($h^2 = 0.56$), although slightly higher, were still moderate (Table 6).

In general,, the CSO families looked straighter, less forked and more vertical than the other origins, except seed lot 4314 (seed source Solomon Islands Arara) for this last trait (Fig. 2a, 2b and 2c). But this distinction did not hold for flowering capacity (Fig. 2d). After 106 months, and despite 62 % of flowering trees recorded for seed lot 1111 (seed source Mata Ayer, Perlis, Malaysia) , more than 70% of trees had not entered the flowering stage for the great majority of the origins assessed. This rate was higher than 90% for 7 Indian provenances, with special mention of seed lots 8367 (Chandrapur Maharastra) and 8824 (Vimoli Vir. Kamataka) which could be distinguished from the other origins by the total absence of flowering trees at that time (Fig. 2d).

Overall, correlations between the various quantitative and qualitative criteria analysed at 49, 61, 72, 85 96 and 106 months after planting indicated weak relationships, except between straightness and bending with values higher than 0.50 (Table 7). At 106 months, phenotypic correlations between growth traits (H and DBH) and quality traits straightness (STR), forkiness (F) and bending (B) were all negative ranging from -0.13 to -0.37, particularly for STR (-0.35, -0.37). At the same time, fork height appeared positively, though weakly (0.26), correlated with flowering.

Discussion

The relatively large number and the diversity of the teak origins included in the present study have allowed the investigation of several aspects of the genetic variation in teak. However, the lack of information on the ultimate origin and on the within-genetic relatedness of certain seed lots hindered more advanced analyses such as genetic correlations. These would have required also a higher number of replicates per lot (Falconer and Mackey 1996; White et al. 2007). The fact that the experiment was not biased by uneven selective thinning during the entire observation period is another advantage compared to other studies (Pedersen et al. 2007).

The overall mortality of 16% after 106 months is low compared to some other experimental teak plantings (Madoffe and Maghembe 1988; Kaosa-ard 2000; Bekker et al. 2004). In addition to a good survival rate, height, DBH and volume increments up to 106 months after planting, appeared also to be noticeably higher than in other locations (Kjaer and Lauridsen 1996). This is more likely due to the positivie influence of the high level of precipitation and the absence of a distinct dry season at the Luasong site (Keiding et al. 1986) than to soil characteristics. According to the literature, these did not look so suitable for teak, partly because of the acidity (Kadambi 1972; Tewari 1992). The diminution of growth rate for height and DBH noticed 49 months after planting might be due to between-tree competition prior to the removal of the buffer. Nonetheless, this operation appeared to have been done at the right stage as no noticeable height or DBH increment was observed thereafter. The significant influence of the various origins tested on height, DBH, fork height and also on the qualitative traits is consistent with observations in other places (Keiding et al. 1986; Dupuy and Verhaegen 1993; Kjaer and Lauridsen 1996). The origin-related differences were however more salient than in Longuza where mean DBH values between origins varied only from 18.8 cm to 20.9 cm after 17 yrs (Madoffe and Maghembe 1988).

The fact that the CSO origins performed in general better in yield and quality than the other seed sources and provenances tested demonstrates the usefulness of CSO for genetic improvement of teak, notwithstanding their constraints and limitations (Kjaer and Foster 1996; Monteuuis and Goh 1999). One of these is the perturbing influence of the trees surrounding the grafted selected genotypes from which the seeds were collected. The fertilization regime in teak is largely allogamic with high outcrossing rates (Kertadijkara and Prat 1995; Kjaer and Suangtho 1995). Between-clone variations in numbers of ramets, flowering capacity, breeding value and synchronism are liable to affect the diversity and performance of families from different clones. One or more of these factors could account for the differences observed between CSO families from the same provenances, such as 9450 and 9446. The tallest CSO families 9450 and 9418 came from the wet Vernoli range and Nilambur provenances of ‘India-moist west coast’ (Keiding et al. (1986), which also performed outstandingly compared to other Indian and Thailand semi-moist provenances tested In Nigeria under a MAR of 2300-2500mm (Keiding et al 1986). The two Solomon Islands seed sources 5212 (Viru) and 4314 (Arara) distinguishable from the others by higher growth and better quality, respectively, originated from places also characterized by heavy annual rainfall. By contrast, drier provenances like Lampang in Thailand and Chandrapur Maharastra in India seemed unsuitable under our site conditions. Overall, seed sources behaved better than provenances. Information on the ultimate origin and relevant rainfall characteristics of the assessed seed sources would have been quite enlightening. This is particularly true for the Solomon Island seed sources in relation to the concept of landrace (Zobel and Talbert 1984). An introduction to Sabah in 1988 of seeds also from the Solomon Islands gave a stand from which 9 selections have been commercially mass produced.,These have been observed to outperform other origins under a wide range of environments on different continents (Monteuuis and Maître 2007; Goh and Monteuuis 2009). The results for 5212 and 4314, and the better CSO families, reported in this paper would suggest that superior clones may be expected from these new sourcesl.

All these observations seem to indicate that, contrary to the general belief, teak can thrive even in the absence of a long distinct dry season during the year. Thus, the species might stand a long period of prolonged drought without necessarily needing it. Natural teak provenances have essentially included sites with high rainfall (MAR > 2,500mm) (Keiding et al 1986). Examples like Java in Indonesia, where teak has been introduced for several centuries, Solomon islands, Costa Rica, Sabah, where the species has behaved surprisingly well under high rainfall and no distinct dry season to become sub-spontaneous, are supportive arguments to this statement (White 1991; Goh et al. 2007; Goh and Monteuuis 2009).

Heritability estimates of the 26 CSO families were limited to the quantitative traits, less subjective and ambiguous than the qualitative ones. The formula used for calculating the heritabilities with 4 as multiplier assumes that families comprise half sibs only, which may result in over estimation if the sibs are more closely related on average. The relevant estimates obtained for height and DBH were similar to those reported by Callister and Collins (2007) who also concluded on moderate narrow sense heritability for these two criteria. Our estimates are also consistent with the heritability values found by Murillo and Badilla (2004) for volume in Costa Rica, and with Danarto and Hardiyanto (2001) in East Java, Indonesia, who obtained a h^2

value of 0.23 for stem diameter at age 12 yrs. According to Gogate et al (1997), the low estimates obtained for heritability of height also reported for many species with possible age-related variations (White et al 2007), might indicate that height in teak is mainly controlled by non-additive gene actions. These low estimates might be due mostly to the noticeable heterogeneity of the site where the trial was set up, as shown by the very highly significant "Replicate" effects pointed out by the statistical analyses (Table 3).

With regard to qualitative criteria, lots like 9450 and 9418 illustrated that fast growing origins could also exhibit good stem straightness (Keiding et al 1986; Kjaer and Lauridsen 1996; Perdersen et al. 2007), despite the negative, although weak correlation found between these two traits (-0.35 at 106 months). According to Kjaer et al (1995) and Pedersen et al (2007), it is interesting to note that stem straightness could be relatively independent from site influence. Our observations and the weak correlation found between fork and flowering indicate that teak can fork, even without flowering, which is well-know to induce in teak fork formation responsible for a tremendous depreciation of its timber value (Keiding et al 1986, Monteuuis et al 1995). The fact that none of the shortest origin trees (8367) had entered the flowering stage yet whereas the tallest origins displayed the higher percentages of trees with flowers is consistent with the ontogenetical concept of ageing (Borchert 1976, Fortanier and Jonkers 1976). This is further supported by the correlation values found between flowering and height, higher than for Callister and Collins (2007). The observation that the majority of the trees of every origin (except seed lot 1111) had not attained the flowering stage after 106 months suggests that the high rainfall conditions of Luasong site are more conducive to vegetative growth than to flowering, known to be stimulated by drier conditions (Keiding et al. 1986).

Conclusions

Luasong trial results confirm the usefulness of a CSO and to a lesser extent of seed sources for the improvement of quantitative and qualitative traits of major economical importance for teak. Besides, they also show the beneficial influence of wet tropical conditions on such traits, notwithstanding the need to take also into consideration the characteristics of the wood produced by such fast growing teak trees, even if some preliminary analyses are encouraging (Bath 2000, Goh et al. 2007). These analyses should be pursued by establishing additional teak origin trials in humid conditions. For the time being, the remarkable genetic diversity of Luasong trial, with the great variation observed among trees within families for different traits, offers good opportunities for selecting outstanding phenotypes. The relevant genotypes, with possible resort to non destructive wood analysis methods for refining the selection (Goh et al. 2007), can be clonally propagated, and after proper testing, wisely deployed to appropriate planting sites to produce high yield and premium quality teak timber. They can also be used as breeding populations, either as CSOs or seedling seed orchards, for advanced generations of genetic improvement (Goh and Monteuuis 2005, 2009).

Acknowledgements: The authors are very grateful to Dr. Garth Nikles for his valuable comments and suggestions on an early draft of this paper.

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Table 1 Characteristics of the 42 teak seed origins compared in Luasong.

Seedlot N°	Origin	Genetic composition of the seeds acquired	Long	Lat	Elevation (m above sea level)	Average annual rainfall (mm)	Average annual temperature (°C)
1111	Ss[1] Malaysia, Mata Ayer, Perlis	na[2]	100°16’E	6° 39’N	50-100	2,000-2,500	27
2222	Ss Malaysia,Segama River Sabah	na	118°18’E	5°6’N	300	2,500	27
4314	Ss Solomon Islands Arara	na	156°30’E	6°40’S	80	3,000	27
5212	Ss Solomon Islands Viru	na	157°46’E	8°28’S	50-100	3,000	27
8367	Prov[3]. India,Chandrapur Maharastra	na	78°46’E	19°30’-20°45’N	na	1,420	na
8668	Prov. Thailand Mae Huat Lampang (natural stand)	na	99°54’E	18°39’N	350	900	27
8669	Ss. Thailand Mae Huat Lampang (planted stand)	na	99°54’E	18°39’N	350	900	na
8822	Prov. India Sakrebail Kamataka	Mixture of 100 OP[4] families	75°29’E	13°48’N	600	898	24
8823	Prov. India, Sakrebail Kamataka	Mixture of 100 OP families	75°29’E	13°48’N	600	1,000	24
8824	Prov. India, Vimoli Vir. Kamataka	Mixture of 100 OP families	74°37’E	15°11’N	600	1,500	26
8831	Prov. India, Karadibetta Kamataka	Mixture of 100 OP families	75°02’E	14°05’N	650	912	24
8832	Prov. India, Gialegundi Kamataka	Mixture of 100 OP families	75°17’E	14°05’N	700	1,000	24
8833	Prov. India, Vimoli Vir. Kamataka	Mixture of 100 OP families	74°37’E	15°11’N	600	1,500	26
8839	Prov. India,Maukal Kamataka	1 OP[4] family	76°00’E	12°15’N	850	1,532	22
8844	Prov. India, Maukal Kamataka	Mixture of 100 OP families	74°37’E	15°09’N	600	1,500	26
9411	CSO[5] Prov. India Nilambur	1 OP family	76°21’E	11°21’N	49	2,900	na
9412	CSO Ss Tanzania Kihuhwi	1 OP family	38°39’E	5°12’S	260	1,880	na
9415	CSO Ss Senegal Djbelor	1 OP family	12°35’N	16°6’W	10	1,640	na
9418	CSO Prov. India Nilambur	1 OP family	na	na	na	2,900	na
9420	CSO Prov. India Nilambur	1 OP family	na	na	na	2,900	na
9424	CSO Ss Tanzania Mtibwa (Morogoro)	1 OP family	37°39’E	6°00’S	460	1,160	na
9426	CSO Ss Tanzania Mtibwa (Morogoro)	1 OP family	37°39’E	6°00’S	460	1,160	na
9430	CSO Prov. Thailand Mae Huat	1 OP family	99°00’E	18°06’N	350	1,300	na
9433	CSO Ss Tanzania Kihuhwi	1 OP family	38°39’E	5°12’S	280	1,860	na
9435	CSO Prov. India Nellicutha	1 OP family	na	na	na	na	na
9436	CSO Prov. India Nellicutha	1 OP family	na	na	na	na	na
9437	CSO Prov. India Nilambur	1 OP family	na	na	na	2,900	na
9440	CSO Prov. India Nellicutha	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
9444	CSO Prov. Thailand Mae Huat	1 OP family	99°00’E	18°06’N	350	1,300	na
9446	CSO Prov. India Vernoli Range	1 OP family	74°35’E	15°10’N	573	2,032	na
9447	CSO Prov. India Nellicutha	1 OP family	na	na	na	na	na
9449	CSO Prov. Thailand Pong Salee	1 OP family	101°01’E	19°08’N	350	1,500	na
9450	CSO Prov. India Vernoli Range	1 OP family	74°35’E	15°10’N	573	2,032	na
9451	CSO Ss Tanzania Bigwa	1 OP family	38°39’E	6°50’S	580	900	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
9456	CSO Prov. India Purunakote	1 OP family	84°00’E	20°00’N	133	1,200-1,500	na
9457	CSO Prov. India Purunakote	1 OP family	84°00’E	20°00’N	133	1,200-1,500	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	26
9999	Ss PNG[6] Ex Brown River	na	147°14’E	9°20’S	400	2,100	26

[1] Ss: seed source, in accordance with Zobel and Talbert (1984)

[2] na: information not available

[3] Prov: provenance, in accordance with Zobel and Talbert (1984)

[4] OP: open pollinated

[5] CSO: clonal seed orchard, La Sangoué, Ivory Coast, longitude: 5°03’W, latitude: 6°16’N, elevation: 200m, average annual rainfall: 1,470mm, average annual temperature: 26°C

[6] PNG Papua New Guinea

Table 2 Descriptions of the Luasong planting site

Lat.	4°35'N
Long.	117°40'W
Elevation (meters above sea level)	130-170
Rainfall regime	2,500 mm MAR without distinct dry season
Mean monthly temperatures	26-28°C
Soil chemical analyses *	
Na (me%)	0.43
K (me%)	0.22
Ca (me%)	1.4
Mg (me%)	1.4
Fe (%)	3.4
Mn (%)	271
P Total (ppm)	187
P Available (ppm)	2.3
Al (me%)	4.32
Org C (%)	0.61
N (%)	0.10
C/N	5.3
pH H_2O (range of variation)	4.8 – 5.6
CEC	12.5
Soil texture*	
Clay (%)	29
Silt (%)	23
Fine sand (%)	40
Coarse sand (%)	8
Soil color	reddish-yellow
Soil classification	Red/yellow latosols

* Average values corresponding to 12 soil samples taken at 0 and 60 cm deep and from six different locations representing the total planted area.

Table 3 Significance levels (P values) of the two experimental factors tested "Replicate" and "Origin" and of their interaction (R x O) on the nine traits assessed for comparing the 42 teak origins at different dates after planting.

Time (months)	**Factors**	**Traits**								
		Mortality	**Height**	**DBH**	**Fork height**	**Volume**	**Straightness**	**Forkiness**	**Bending**	**Flowering**
13	Replicate (R)	< 0.0001	< 0.0001	< 0.0001	na[1]	< 0.0001	na	na	na	na
	Origin (O)	< 0.0001	< 0.0001	< 0.0001	na	< 0.0001	na	na	na	na
	R X O	-	< 0.0001	< 0.0001	na	< 0.0001	na	na	na	na
35	Replicate (R)	< 0.01	< 0.0001	< 0.0001	na	< 0.0001	na	na	na	na
	Origin (O)	NS	< 0.0001	< 0.0001	na	< 0.0001	na	na	na	na
	R X O	-	< 0.0001	< 0.0001	na	< 0.0001	na	na	na	na
49	Replicate (R)	< 0.001	< 0.0001	< 0.0001	na	< 0.0001	< 0.0001	NS	< 0.001	< 0.01
	Origin (O)	< 0.05	< 0.0001	< 0.0001	na	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
	R X O	-	< 0.0001	< 0.0001	na	< 0.0001	< 0.0001	< 0.001	< 0.0001	< 0.001
61	Replicate (R)	< 0.01	< 0.0001	< 0.0001	na	< 0.0001	< 0.0001	< 0.0001	< 0.05	NS
	Origin (O)	< 0.05	< 0.0001	< 0.0001	na	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
	R X O	-	< 0.0001	< 0.0001	na	< 0.0001	< 0.0001	NS	< 0.0001	< 0.0001
72	Replicate (R)	NS	< 0.0001	< 0.0001	na	< 0.0001	< 0.0001	< 0.05	< 0.0001	< 0.01
	Origin (O)	NS	< 0.0001	< 0.0001	na	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
	R X O	-	< 0.0001	< 0.0001	na	< 0.0001	< 0.0001	< 0.05	< 0.0001	< 0.0001
85	Replicate (R)	< 0.0001	< 0.0001	< 0.0001	na	< 0.0001	< 0.001	< 0.0001	< 0.0001	< 0.0001
	Origin (O)	NS	< 0.0001	< 0.0001	na	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
	R X O		< 0.0001	< 0.0001	na	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
96	Replicate (R)	NS	< 0.0001	< 0.0001	na	< 0.01	NS[2]	< 0.01	< 0.01	NS
	Origin (O)	< 0.0001	< 0.0001	< 0.0001	na	< 0.0001	< 0.0001	< 0.0001	< 0.01	< 0.0001
	R X O	-	< 0.0001	< 0.0001	na	< 0.0001	< 0.0001	< 0.01	< 0.0001	< 0.0001
106	Replicate (R)	NS	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.01	< 0.0001	< 0.0001
	Origin (O)	< 0.01	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
	R X O	-	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	NS	< 0.0001	< 0.0001

[1] na: information not available
[2] NS: not significant (P > 0.05)

Table 4 Number of trees recorded (N), relevant mortality (M) and mean values 106 months after planting for the four quantitative traits assessed and compared for the 42 teak origins (CSO in grey cells) planted in Luasong., Data are completed by minimal (Min), maximal (Max) and coefficient of variation (CV in %) values.

Seed lot N°	N	M (%)	Height (m)				DBH (cm)				Volume (dm^3)				Fork height (m)			
			Min	Max	Mean	CV	Min	Max	Mean	CV	Min	Max	Mean	CV	Min	Max	Mean	CV
1111	39	13	8.0	27.2	16.9	22	8.0	23.0	16.3	20	17.8	283	147	47	1.3	12.0	4.8	48
2222	41	9	7.2	22.2	15.7	20	7.5	21.0	15.5	24	14.4	260	129	51	0.8	7.0	3.7	46
4314	44	2	7.6	23.4	18.2	17	7.0	25.5	19.0	23	13.1	405	215	47	2.0	14.5	6.7	41
5212	37	18	12.0	27.0	19.0	16	9.0	32.5	20.3	26	31.0	664	258	56	2.2	16.5	7.0	47
8367	37	18	4.5	16.0	10.7	30	4.5	17.0	11.0	29	4.7	132	50	67	0.6	7.0	3.5	42
8668	36	20	8.0	21.8	16.1	18	8.5	24.0	14.7	25	22.5	332	117	59	1.0	9.2	4.4	44
8669	33	27	2.0	19.6	13.6	29	3.5	19.0	11.6	31	1.5	176	69	69	0.8	7.3	3.4	51
8822	32	29	6.4	22.8	14.6	32	7.0	24.5	16.1	30	15.1	399	144	74	0.5	8.0	5.2	31
8823	41	9	7.8	24.4	16.3	22	7.0	29.5	15.6	33	13.3	615	143	83	2.0	11.0	5.2	42
8824	36	20	9.0	26.0	15.6	28	9.0	24.5	16.1	24	25.0	343	134	60	1.9	13.4	5.6	53
8831	39	13	7.8	23.0	15.4	21	7.5	23.5	14.4	28	15.3	272	113	64	1.3	11.0	5.2	45
8832	40	11	9.4	26.0	16.8	23	8.5	21.5	14.8	24	22.7	322	126	60	2.3	10.5	5.4	40
8833	37	18	9.0	26.0	16.9	22	7.5	26.5	17.1	26	17.7	487	169	62	1.3	10.0	5.4	37
8839	27	40	7.0	24.4	17.0	30	7.0	22.0	15.3	30	14.1	342	141	63	1.0	13.0	5.4	56
8844	39	13	11.0	24.0	16.0	21	8.5	25.5	16.6	26	27.6	422	152	65	1.6	11.5	5.3	48
9411	41	9	12.8	23.0	18.0	14	12.0	28.0	19.5	22	65.5	464	225	52	0.0	15.0	8.1	49
9412	39	13	14.4	28.0	20.4	15	11.0	29.0	19.8	25	53.9	629	259	57	1.0	17.5	7.2	43
9415	38	16	10.0	22.6	17.8	19	8.0	29.0	19.4	24	23.5	481	226	53	1.5	12.7	6.9	42
9418	41	9	11.8	28.8	20.6	18	10.0	26.5	19.7	21	37.7	577	253	46	2.5	14.5	8.2	42
9420	39	13	12.0	26.0	16.4	19	8.0	26.5	16.5	25	24.5	397	150	58	2.2	11.8	5.9	38
9424	43	4	9.0	24.0	17.0	21	7.5	25.5	17.2	24	17.1	453	167	55	0.6	9.3	4.8	44
9426	42	7	8.0	24.8	18.3	21	8.5	33.0	18.8	28	20.4	764	223	65	2.3	15.0	7.0	42
9430	38	16	11.0	26.6	19.5	17	9.0	32.5	19.9	24	28.8	614	248	50	4.0	9.5	5.9	26
9433	42	7	6.0	22.0	15.2	25	8.0	26.0	16.9	27	17.4	357	152	56	1.5	7.5	4.6	35
9435	36	20	10.2	22.0	17.5	17	10.5	29.5	18.3	23	45.0	447	193	52	1.3	9.5	5.2	36
9436	30	33	6.5	24.4	18.0	19	5.0	26.0	18.7	25	6.0	442	210	55	0.5	9.5	5.7	37
9437	41	9	11.2	28.4	19.4	23	11.5	30.0	19.5	24	47.8	551	241	55	1.3	14.1	7.7	48
9440	42	7	13.2	23.2	18.0	11	11.5	29.0	18.6	23	57.5	498	202	51	1.4	9.3	4.7	41
9443	39	13	6.4	21.8	13.6	33	7.0	27.5	15.7	32	11.6	483	132	84	1.5	8.5	4.6	43
9444	38	16	13.6	20.6	18.2	9	10.0	26.5	19.3	21	42.4	419	214	45	2.4	12.2	6.5	40
9446	34	24	8.0	24.0	17.5	22	8.0	28.0	17.4	31	17.8	521	190	69	0.9	12.5	5.4	58
9447	39	13	4.2	24.6	18.1	25	6.0	31.5	19.5	31	6.4	665	243	67	0.7	11.0	6.1	44
9449	34	24	11.8	24.2	19.6	15	10.5	34.5	21.1	23	41.6	760	278	52	1.9	10.7	7.1	28
9450	45	0	9.2	29.0	21.1	15	5.5	30.5	20.3	23	9.3	609	276	47	3.5	15.5	9.6	38
9451	38	16	10.6	25.2	18.1	20	10.5	25.0	16.8	22	45.0	455	165	58	2.1	7.0	4.7	27
9452	41	9	5.0	22.2	15.2	26	8.0	24.5	16.1	26	12.7	299	138	59	1.0	10.3	4.5	47
9454	40	11	9.0	23.4	15.8	18	9.0	26.5	15.8	22	27.4	349	128	50	1.6	9.5	5.0	44
9456	38	16	12.0	20.8	16.9	14	7.5	26.5	16.9	26	23.0	430	161	60	1.3	11.1	5.1	48
9457	36	20	12.0	22.4	16.2	15	10.0	23.5	16.3	24	38.2	344	143	57	1.0	8.3	5.2	32
9459	38	16	11.0	26.0	18.6	25	10.0	32.5	19.4	28	35.6	747	246	70	1.2	9.2	5.0	37
9463	41	9	10.0	31.2	20.2	21	9.0	30.0	18.7	27	26.7	768	238	68	2.2	12.0	6.1	33
9999	35	22	7.0	20.6	14.3	19	7.0	22.0	15.3	25	12.3	249	116	57	1.0	6.0	3.4	37
Mean	38	16	9.1	24.1	17.1	21	8.3	26.6	17.3	26	25.0	458	179	59	1.5	11.0	5.6	42

Table 5 Phenotypic correlation coefficients R ($P \leq 0.001$) for height (H), diameter at breast height (DBH) and fork height (FH) recorded at different ages for the population of the 42 teak origins mixed.

Criteria/Age (in months)	H13	DBH13	H35	DBH35	H49	DBH49	H61	DBH61	H72	DBH72	H85	DBH85	H96	DBH96	H106	DBH106
DBH13	0.94															
H35	0.66	0.62														
DBH35	0.77	0.75	0.81													
H49	0.51	0.48	0.70	0.72												
DBH49	0.55	0.54	0.62	0.82	0.81											
H61	0.50	0.45	0.67	0.68	0.89	0.77										
DBH61	0.54	0.52	0.62	0.81	0.81	0.96	0.79									
H72	0.49	0.45	0.66	0.69	0.88	0.78	0.90	0.81								
DBH72	0.51	0.49	0.61	0.79	0.80	0.94	0.79	0.98	0.80							
H85	0.40	0.34	0.56	0.59	0.75	0.67	0.76	0.69	0.81	0.69						
DBH85	0.48	0.46	0.61	0.76	0.80	0.92	0.80	0.96	0.81	0.98	0.70					
H96	0.36	0.32	0.56	0.55	0.74	0.65	0.77	0.69	0.79	0.70	0.73	0.72				
DBH96	0.46	0.44	0.60	0.75	0.79	0.91	0.80	0.96	0.81	0.97	0.70	0.98	0.77			
H106	0.34	0.30	0.53	0.57	0.72	0.66	0.71	0.68	0.74	0.68	0.70	0.69	0.75	0.71		
DBH106	0.46	0.44	0.60	0.74	0.79	0.89	0.80	0.93	0.81	0.96	0.70	0.97	0.74	0.98	0.70	
FH106	0.26	0.23	0.44	0.36	0.54	0.40	0.56	0.43	0.55	0.44	0.47	0.46	0.60	0.48	0.55	0.48

Table 6 Heritabililty (narrow sense, h^2) average estimates with standard error between brackets for height, DBH, volume and fork height recorded at different ages for the 26 CSO families.

Age (month)	Height	DBH	Volume	Fork Height
13	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	*
35	0.16 (±0.07)	0.07 (±0.04)	0.13 (±0.06)	*
49	0.26 (±0.09)	0.04 (±0.04)	0.12 (±0.06)	*
61	0.30 (±0.10)	0.10 (±0.05)	0.17 (±0.07)	*
72	0.37 (±0.11)	0.16 (±0.07)	0.23 (±0.08)	*
85	0.50 (±0.14)	0.18 (±0.07)	0.28 (±0.09)	*
96	0.48 (±0.14)	0.24 (±0.09)	0.34 (±0.11)	*
106	0.51 (±0.14)	0.24 (±0.08)	0.34 (±0.11)	0.56 (±0.16)

*: data non available.

Table 7 Phenotypic correlation coefficients for height (H), diameter at breast height (DBH), straightness (STR), forking (F), bending (B), flowering (FLO) and fork height (FH) measured at 106 months established from records taken 49, 61, 72, 85, ,96 and 106 months after planting for the 42 teak origins as a whole; NS: values not indicated as not statistically significant (P > 0.05); *: significant at 0.001 < P ≤ 0.05, whereas other values are statistically significant at P ≤ 0.001.

	After 49 months				After 61 months				After 72 months				After 85 months				After 96 months				After 106 months				
Criteria	**STR49**	**F49**	**B49**	**FLO49**	**STR61**	**F61**	**B61**	**FLO61**	**STR72**	**F72**	**B72**	**FLO72**	**STR85**	**F85**	**B85**	**FLO85**	**STR96**	**F96**	**B96**	**FLO96**	**STR106**	**F106**	**B106**	**FLO106**	**FH106**
H	-0.40	-0.22	-0.42	0.08	-0.35	-0.18	-0.35	0.05*	-0.36	-0.18	-0.29	0.17	-0.38	-0.13	-0.20	0.06*	-0.36	-0.20	-0.34	0.16	-0.35	-0.24	-0.30	0.29	0.55
DBH	-0.30	-0.13	-0.30	0.11	-0.29	-0.07	-0.26	0.11	-0.32	-0.08	-0.19	0.26	-0.31	-0.04*	-0.19	0.14	-0.29	-0.09	-0.28	0.26	-0.37	-0.13	-0.25	0.32	0.48
STR		0.41	0.66	NS		0.57	0.69	NS		0.26	0.60	-0.07		0.32	0.45	-0.05*		0.33	0.50	-0.08		0.27	0.58	-0.08	-0.33
F			0.33	0.06*			0.47	NS			0.27	NS			0.26	NS			0.41	NS			0.33	-0.08	-0.41
B				NS				NS				NS				-0.13				-0.08				-0.11	-0.40
FLO																									0.26

Fig. 1a Assessment of the time course variations of height for each of the 42 teak origins (CSO indicated by solid lines)

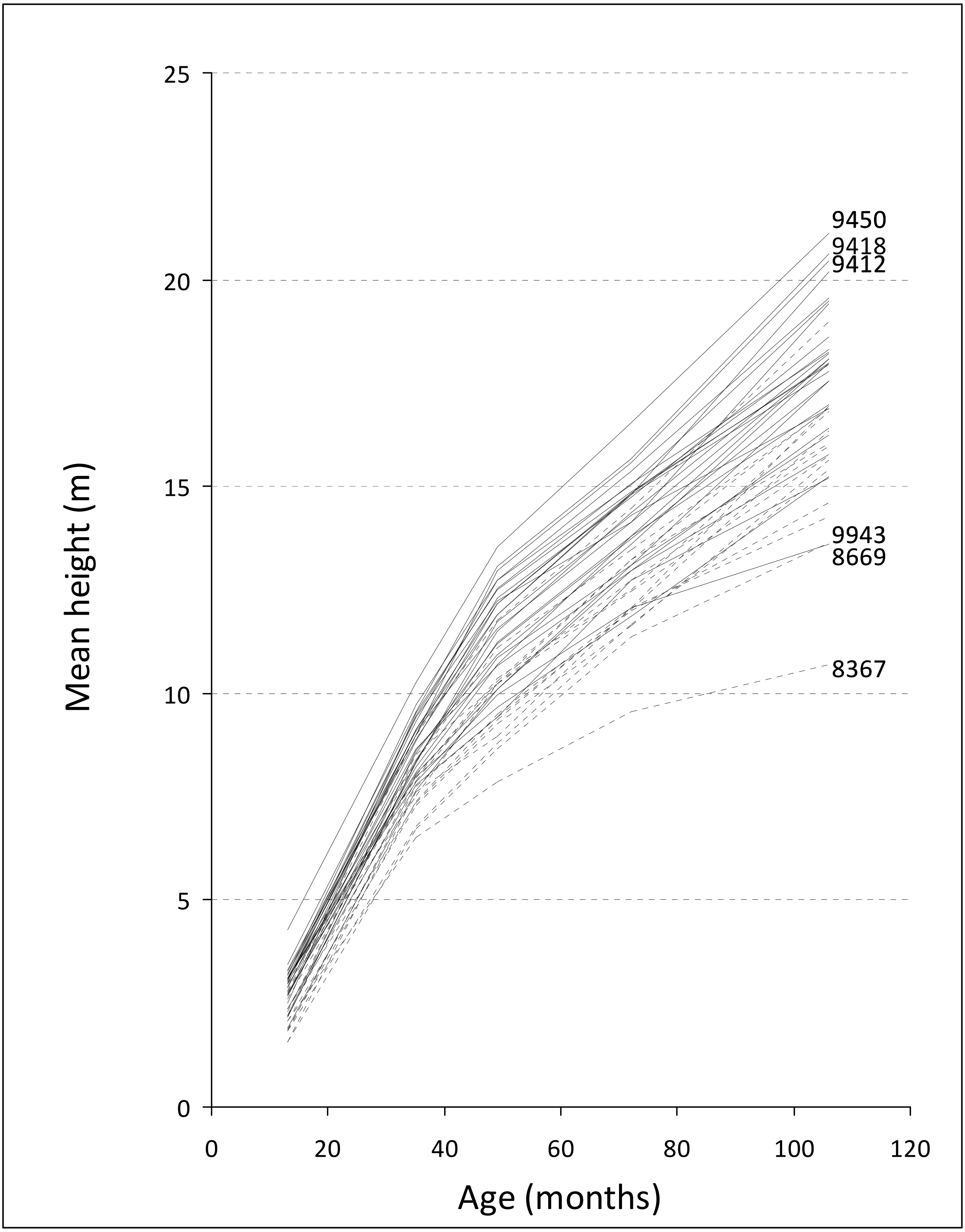

Fig. 1b Assessment of time course variations of DBH for each of the 42 teak origins (CSO indicated by solid lines).

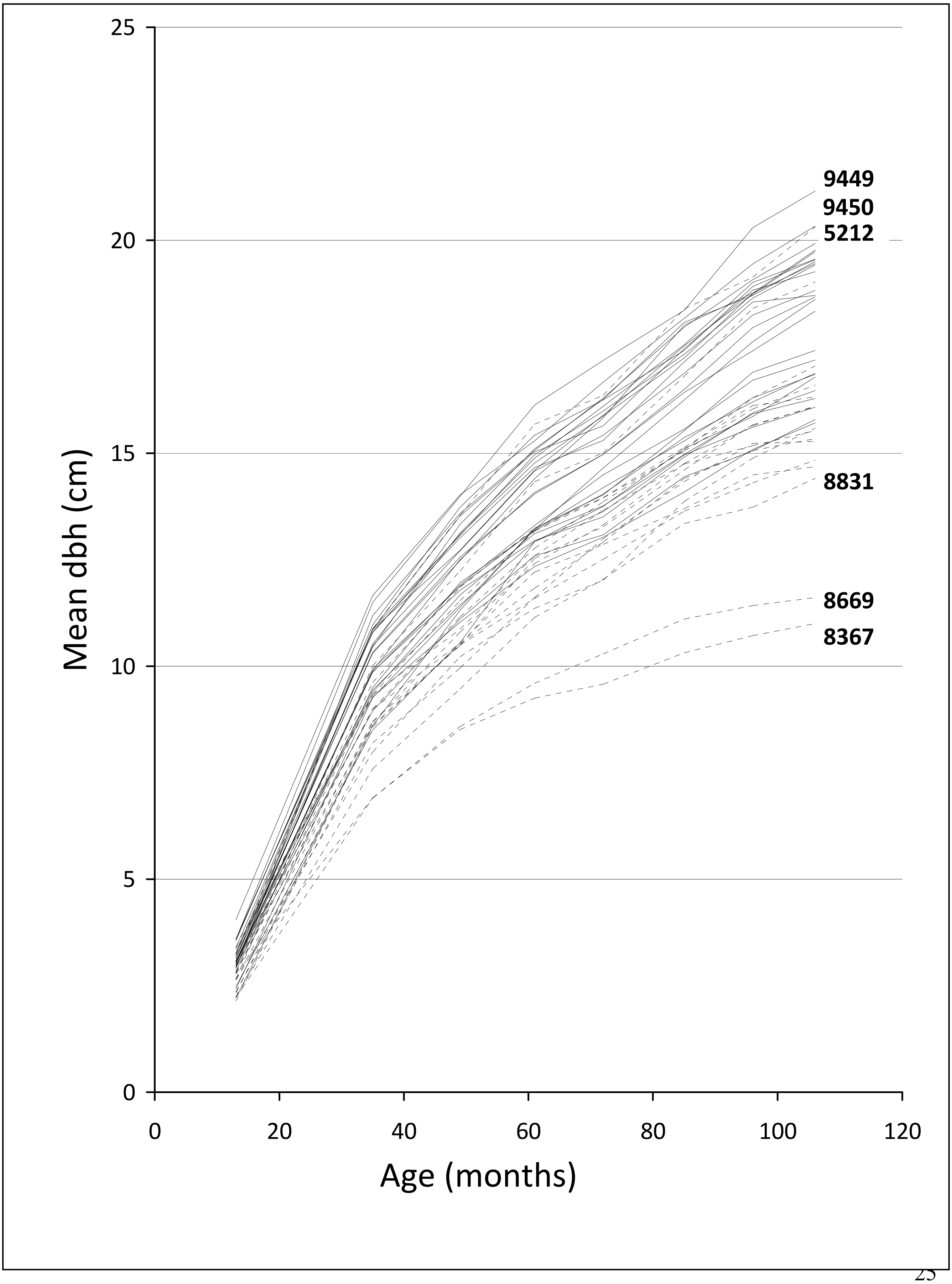

Fig. 1c Assessment of time course variations of bole volume for each of the 42 teak origins (CSO indicated by solid lines).

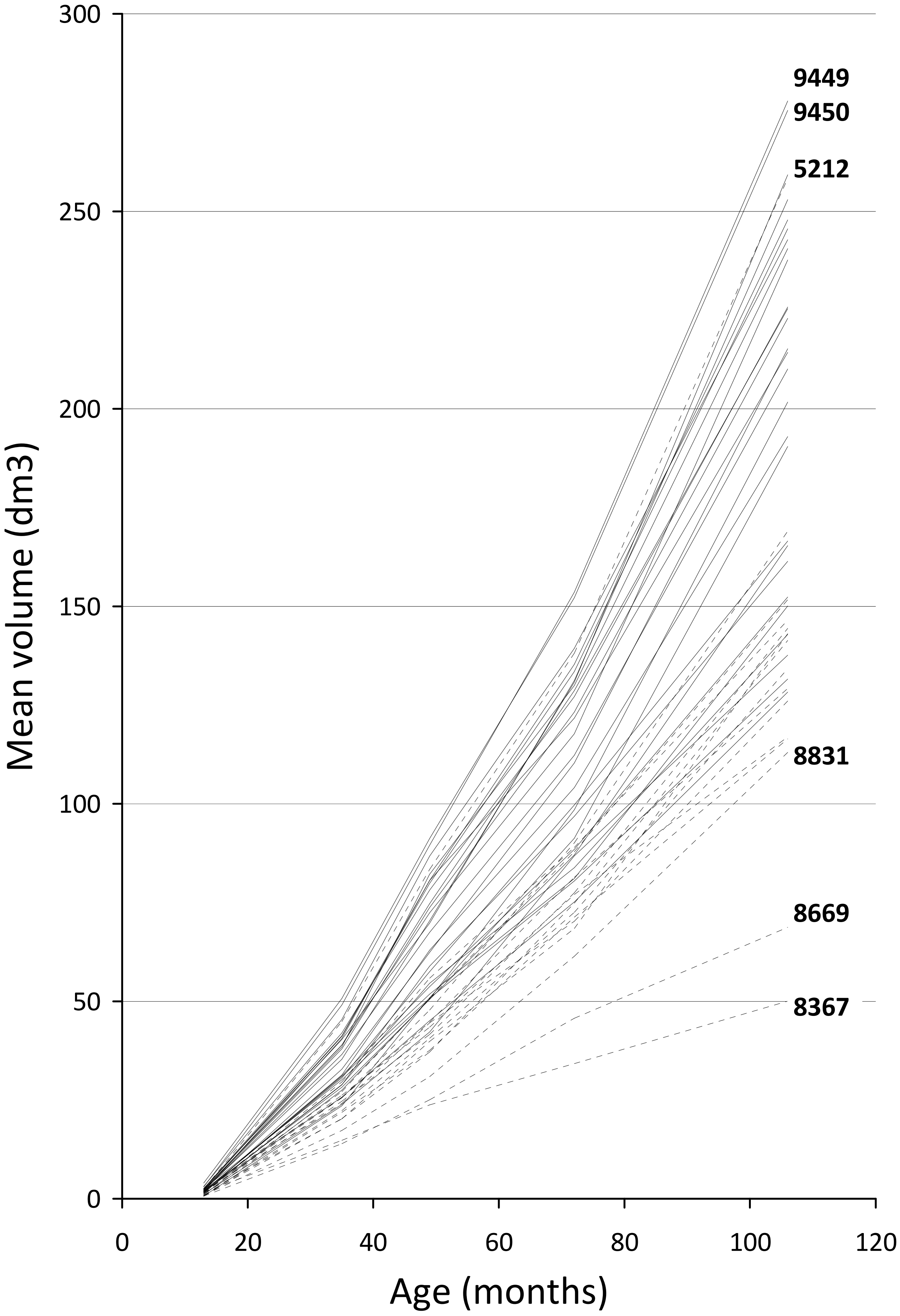

Fig. 2a Proportion (%) of straight trees (score 1 for straightness) for all origins (CSO in dark bars) assessed 106 months after planting.

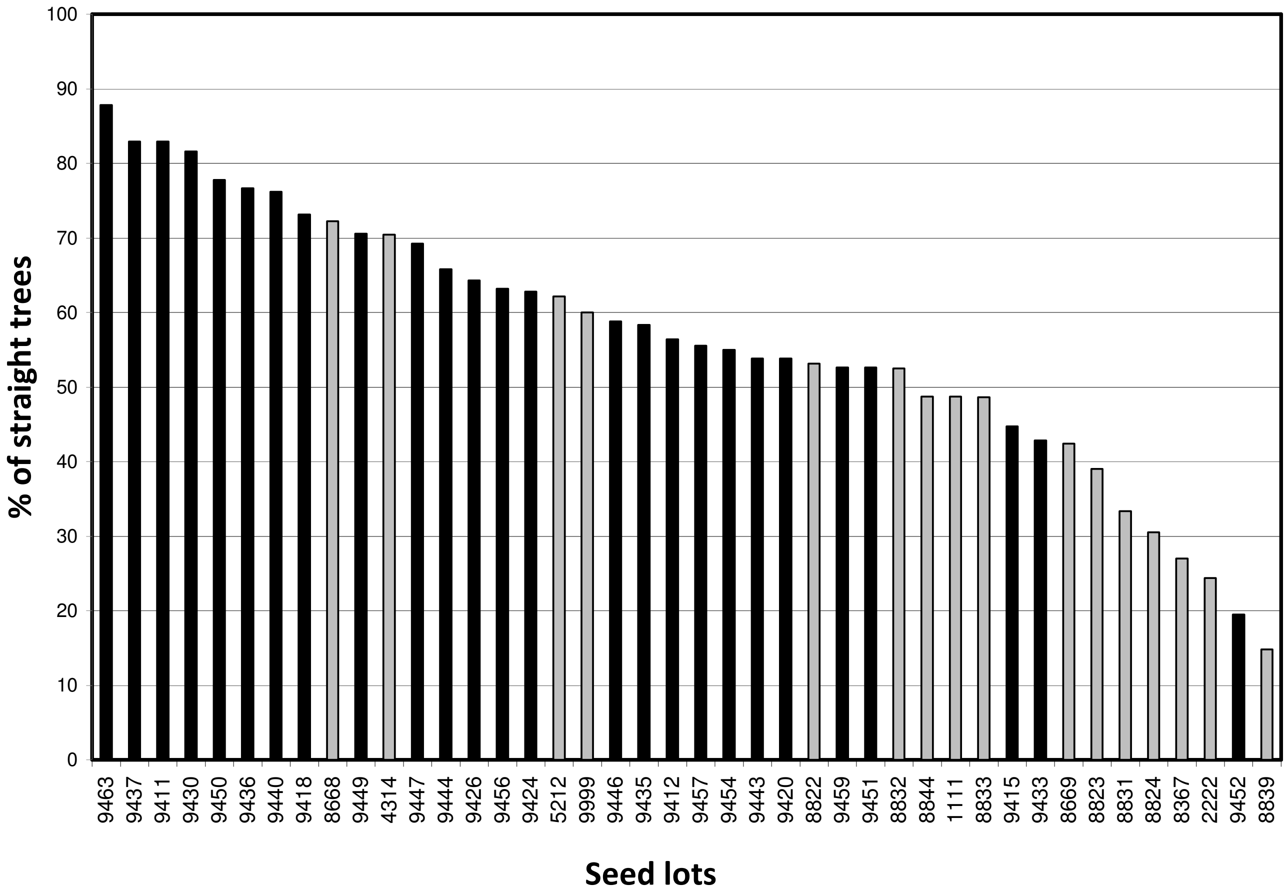

Fig. 2b Proportions (%) of trees without any fork (score 1 for forkiness) for all origins (CSO in dark bars) assessed 106 months after planting.

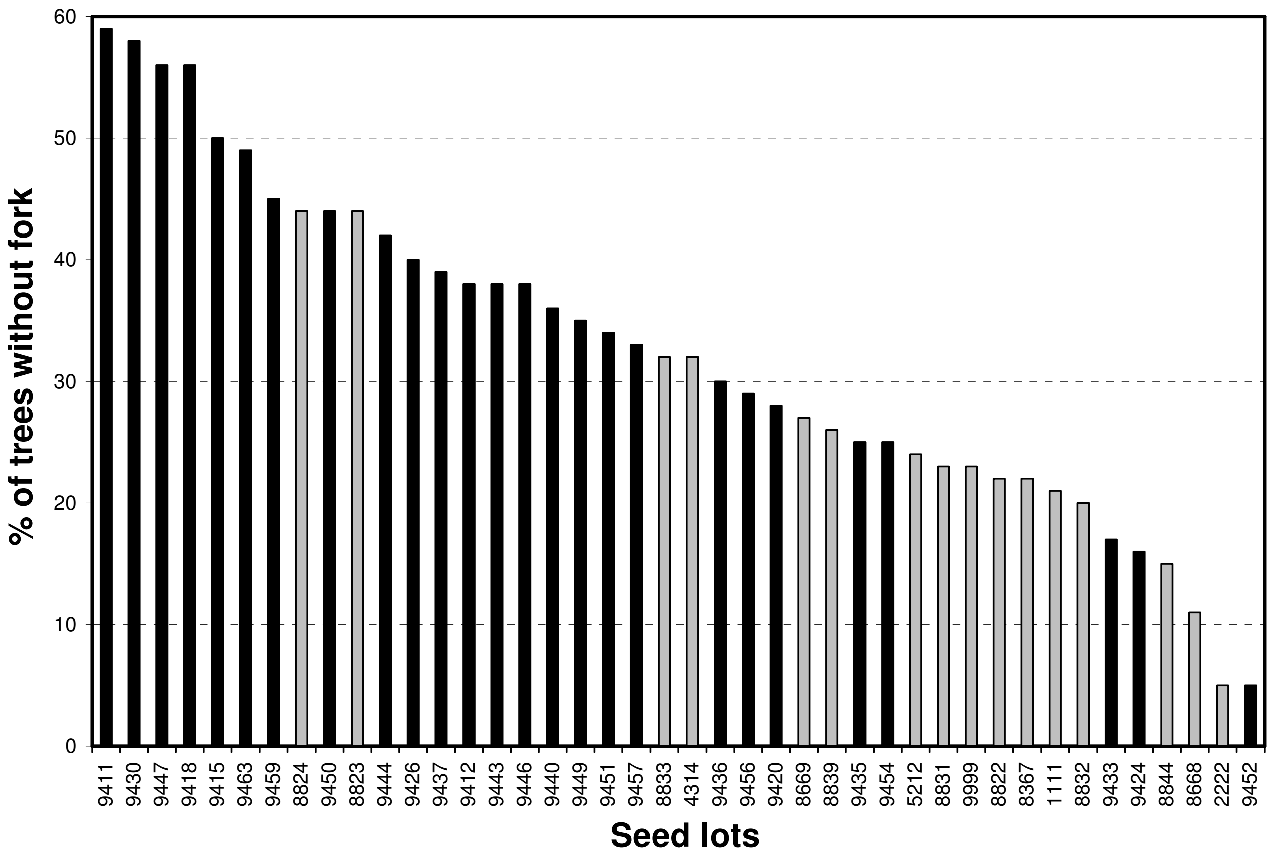

Fig. 2c Proportions (%) of vertical trees (score 1 for bending) for all origins (CSO in dark bars) assessed 106 months after planting.

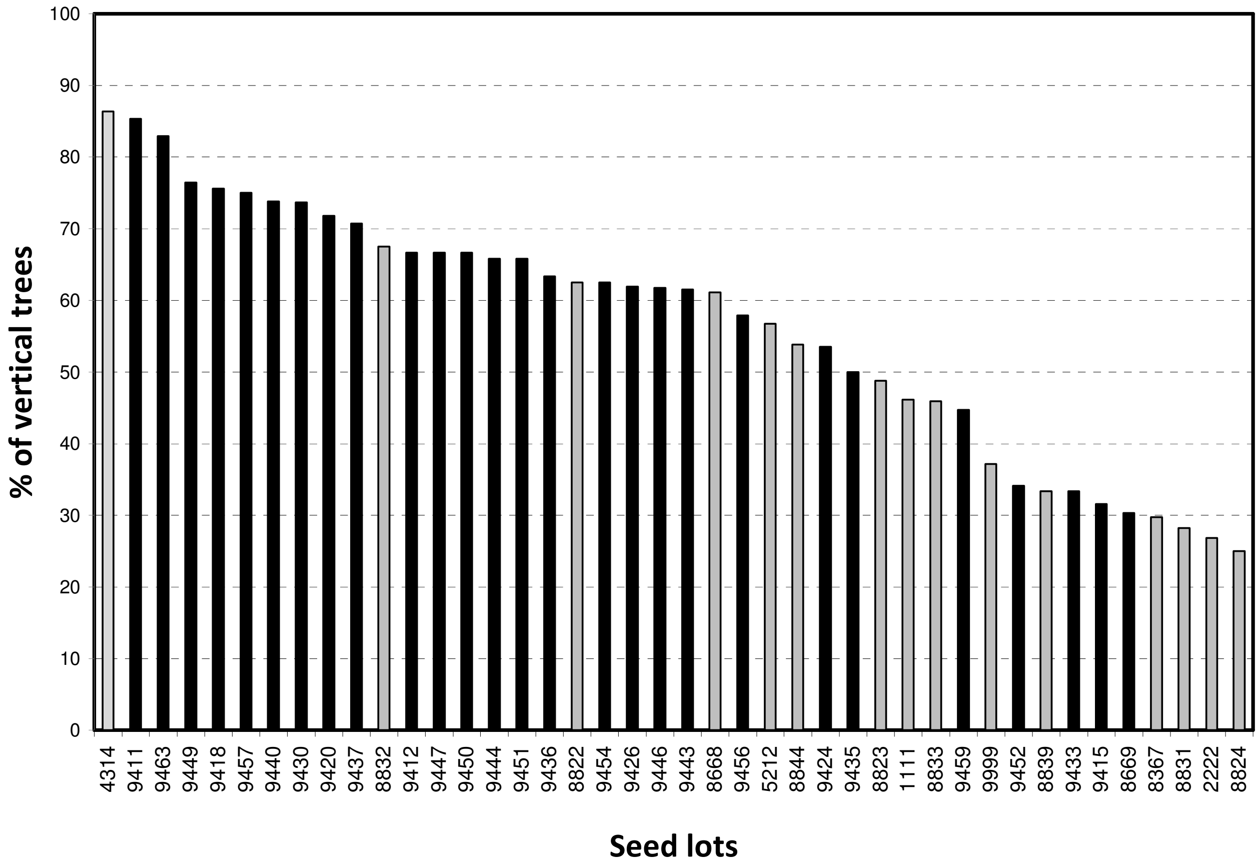

Fig. 2d Proportions (%) of trees without any flower (score 1 for flowering) for all origins (CSO in dark) assessed 106 months after planting.