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ORIGINAL PAPER

Provenance effect on the ring structure of teak (*Tectona grandis* L.f.) wood by X-ray microdensitometry

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Abstract
• ***Context*** Teak (*Tectona grandis* L.f.) is a tropical timber which is appreciated worldwide and has been planted into many regions of the tropics. It is essential to obtain information about provenance variation of basic wood properties in order to preserve the wood quality of end-products derived from future plantations. Figuring is one of the wood characteristics valued for panelling and furniture and it is an important parameter to evaluate the quality of teak wood. The ring structure affects within-ring and between-ring colour variation and, therefore, the figure of wood and the related aesthetical aspects.
• ***Methods*** By means of microdensity profiles, we constructed a segmented linear model that depicts the anatomical structure of the rings. It effectively distinguished ring porous and diffuse porous rings, leading to the development of an efficient ring porosity index, further used to study the provenance variation of the ring structure.
• ***Results*** A significant provenance effect was detected for both wood density variables and ring anatomical structure. Although no correlation was detected between the ring structure and the precipitation level at the provenance origin, the two provenances from very wet climates were distinguished by low values of ring porosity index (diffuse porous ring).
• ***Conclusion*** The progenies in our study, collected from origins with various climates, planted in a new climate, seem to maintain to some extent the wood characteristics typical of their mother trees, suggesting that these ring characteristics may be inherited.

Keywords *Tectona grandis* · Wood anatomy · Aesthetic value · Wood quality · Provenances

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1 Introduction

Teak (*Tectona grandis* L.f.) is a highly valued tropical timber tree with a natural area ranging from India to Thailand and Laos. Its wood is used for heavy construction as well as for fine furniture. It has been therefore introduced from different parts of its natural range into many regions of the tropics in Africa and America (Behaghel 1999; Kokutse et al. 2004). International provenance tests (replicated trials) have been installed as the first steps of future tree improvement programs, in order to select the provenances best adapted to the regions of introduction. The first provenance tests were installed in south-east Asia and in Africa during the 1960s and the 1970s (Egenti 1978; Hedegart 1974; Vivekanandan 1977). Studies showing a significant provenance effect for different traits were published from the end of the 70's up to the present: for example, a significant provenance effect was found for survival (Hidalgo et al. 1986; Madoffe and Maghembe 1988), growth (Egenti 1977, recd. 1980; Hidalgo et al. 1986; Jayasankar et al. 1999, 2003; Madoffe and Maghembe 1988) and different characters of stem form (Egenti 1977, recd. 1980; Rao et al. 2001). In one case, no significant provenance effect was observed for height and diameter growth (Rao et al. 2001).

It is essential to obtain information about the provenance variation in basic wood properties in order to preserve the wood quality of end-products made from timber from future plantations. According to our knowledge, the only wood properties for which a significant provenance effect was found and published to date are heartwood content and wood mineral content (Kjaer et al. 1999). No provenance effect based on the analysis of replicated trials has been published for important basic wood properties like wood density or wood anatomy. Geographical variation of wood density and wood anatomy was found by Varghese et al. (2000), by Bhat and Priya (2004) and Macchioni et al. (2007), as well as in older studies cited by these authors. But due to the lack of genetic trial, environmental and genetic factors are confounded and cannot be separated in these studies.

Finally, contradictory results were reported at clone level: if a significant clone effect was found by Indira and Bhat (1998) and Bhat and Indira (2005) for several physical and anatomical wood traits such as ring width, wood density, vessel diameter and fibre wall thickness, a low value of broad sense heritability and no significant difference among clones was reported by Bhat (2000) for specific gravity.

The objective of this article is to present and discuss some results about provenance variation of important basic wood properties having an influence on teak wood quality. Obviously, wood anatomy is one of them (Bhat et al. 2001; Bhat and Priya 2004; Kokutse et al. 2009; Rajput et al. 2005) as it strongly affects the aspect of teak wood and its aesthetic value. Efficient assessment of provenance variation requires collection of a large number of samples and, at the same time, wood anatomy observations are tedious and time consuming. A well-known alternative to direct wood anatomy measurements is X-ray wood microdensity (Polge 1978). Density is an indirect measurement of the proportion of cell wall and cell lumen in a wood sample (Zobel and van Buijtenen 1989). Radial microdensity profiles have been found to be strongly related with radial profiles of tracheid anatomy in conifers (Decoux et al. 2004; Rathgeber et al. 2006). However, in some hardwoods species like oak, because of a high within-ring tangential variability of wood anatomy, it has been found difficult to establish a simple relationship between microdensity and anatomy (Degron and Nepveu 1996). Conversely, other results show that in diffuse porous or ring porous species with low tangential variation of wood anatomy, there is a strong or quite strong relationship between radial microdensity variation and radial variation of vessel characteristics (Roque and Tomazelo-Filho 2007). According to our knowledge, no result has been published about such a relationship in teak. However, because of the very small tangential variation of wood anatomy (compared to other broadleaves species like oak, Détienne pers. com.), we assume for teak that radial microdensity profiles accurately describe radial variation of anatomy, particularly radial variation of the lumen area of vessels.

Teak is said to be a ring porous hardwood (Purkayastha 1996; Titmuss 1971), but the pore ring can be sometimes not very well developed leading to a semi ring porous or, in some samples, to a diffuse porous wood (Jane 1970; Priya and Bhat 1999). The first part of the ring generally contains a narrow band of abundant, large lumen vessels and it is therefore the lowest density part of the ring. Then, the abundance and the lumen area of vessels more or less gradually decrease to a minimum value toward the end of the ring, jointly with a density increase (Fig. 1). Visual observation and comparison of teak ring microdensity profiles and of teak ring anatomy suggests that ring structure can be efficiently described using a simple linear model. In this article we propose develop such a model and to relate its parameters to the porosity of teak rings. Porosity (vessel arrangement), together with ring width and distribution of earlywood and latewood, affects within- and between-ring colour variation and, therefore the veining of wood and the related aesthetical aspects. Veining is one of the wood characteristics appreciated and valued for panelling and furniture thanks to the figures produced on the longitudinal surfaces and, therefore is an important measure of teak wood quality. The ring porous structure emphasizes the veining of wood (and therefore the figure), contrary to the diffuse porous structure that makes the appearance of the surfaces more homogeneous.

Previous works reported a significant influence of the water availability and rainfall at the growth site on the ring anatomical structure of teak wood: Priya and Bhat (1999) observed that irrigated plants had a diffuse porous structure whereas non-irrigated plants had a typical ring porous structure. The same trend is observed by Macchioni et al. (2007) who noticed that teak plantation trees growing under wet climate had a diffuse porous structure while the same plant material growing under dry climate had a ring porous structure. In the present work, we investigated also the effect of the rainfall level of the regions of origin on the ring anatomical structure of the provenances. Therefore, our objective is to test the hypothesis that there is a significant provenance effect on the microdensity variables and on the ring structure of teak and that there exist a relation between this provenance effect and the rainfall level in the provenance regions of origin.

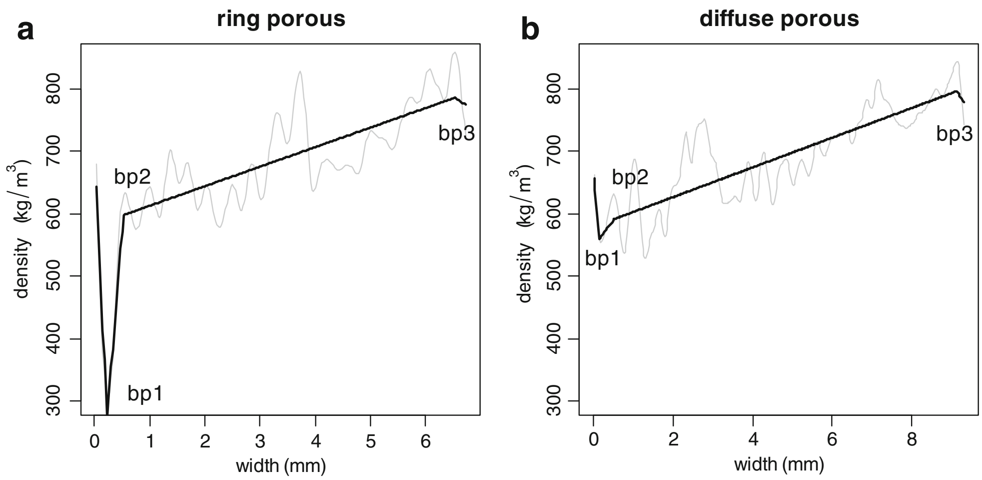

Fig. 1 Two examples of four segmented linear regression: a model of typical ring porous (**a**) and diffuse porous ring (**b**)

Hence, first, we investigate provenance variation for commonly used within-ring microdensity variables. Then we use the microdensity profiles to construct an original model (straight lines model) describing the ring structure (from ring porous type to diffuse porous type) and we use it to study the provenance variation for ring structure and thus, indirectly, the effect of such variation on the aesthetic value of teak. Finally, we relate the ring structure to the rainfall of the region of origin of the provenances.

2 Materials and Methods

2.1 Site, sampling and material description

The sampled site is part of an international series of teak provenance trials, previously assessed and reported by Keiding et al. (1986) and Kjaer et al. (1995). It is located in Tain, Ghana (lat. 7° 30′N, long. 2° 30′W; elevation 100 ma.s.l.) in a dry semi-deciduous forest vegetation zone (1,140 mm of annual rainfall). The plantation was established in 1972 with 12 provenances, four replicates and one provenance with two replicates; the experimental unit was a 7×7 square plot. In Table 1 the information about the geographic origin of all the provenances is reported, including the annual rainfall. According to the results based on neutral molecular markers and reported by Fofana et al. (2009) and Verhaegen et al. (2009), Ghana and Indonesia provenances are strictly linked to those of Laos origin, forming a single group; while the provenances 3,021 and 3,022 belong to the South India group.

Two to seven trees were sampled for each provenance (Table 2); one increment core per tree was collected at 1.3 m above the ground level on a random orientation and the corresponding stem diameter was measured.

Table 1 Description of the provenances: region, country, provenance name, geographic coordinates, elevation and annual precipitations

Code	Region	Country	Provenance name	Latitude	Longitude	Elevation (m a.s.l.)	Precipitation (mm)
3021[a]	Indian moist coast	India	Nilambur	11°21′N	76°21′E	49	2,565
3022[a]	Indian dry interior	India	Bairluty 1	15°51′N	78°45′E	305	1,016
3044[a]	West Africa	Ghana	Jema	7°50′N	1°50′W	210	1,200
SG1		Ghana	Landrace	7°50′N	1°50′W	267	1,100–1,600
SG3		Ghana	Landrace	7°50′N	1°50′W	267	1,100–1,600
SG4		Ghana	Landrace	7°50′N	1°50′W	267	1,100–1,600
3047[a]	Indonesia	Indo-PNG	Bangsri, Pati	6°30′S	110°48′E	75–100	3,900
3048[a]		Indo-PNG	Nanas, Blora	6°57′S	111°30′E	250–280	1,700
3049[a]		Indo-PNG	Ngliron, Ngliron	7°12′S	111°22′E	150	1,200
3050[a]		Indo-PNG	Temandsang	7°12′S	111°22′E	104	1,200
3055[a]	Laos	Laos	Savannakhet	16°33′N	104°45′E	100	1,309
3056[a]		Laos	Savannakhet	16°33′N	104°45′E	100	1,309
3059[a]		Laos	Vientiane Town	17°56′N	102°37′E	50–100	1,569

[a] Number designated by Danida Forest Seed Centre

Table 2 Number of sampled trees (one core per tree), minimum, maximum and mean diameter at breast height per provenance

Provenance	Core N.	Mean diameter (cm)	Min/max diameter (cm)
3021	6	27	21–32
3022	5	27	22–32
3044	5	26	25–29
SG1	6	24	20–28
SG3	3	23	23–24
SG4	4	20	6–26
3047	5	25	21–31
3048	4	23	22–26
3049	5	27	24–29
3050	4	27	22–32
3055	7	23	13–28
3056	6	25	21–31
3059	2	27	22–31

From each core a thin section was prepared along the tree radius. The sections were approximately 1 cm large on the tangential direction and 1.20 mm thick on the longitudinal direction; they were prepared and then seasoned at 20°C and 65% R.H. before being X-rayed (Polge 1978). The resulting X-ray films were scanned at a 1,000 dpi resolution with 8 bits per pixel and the digital images were then processed with the WinDENDRO software (Guay et al. 1992), obtaining a spatial resolution of 25 μm. The data processing was performed by using computer routines written in the R statistical programming language (R Development Core Team 2010).

2.2 Microdensity measurements

The microdensity profiles were cross-dated and, thanks to the known sampling year and the occurrence of clear annual rings, each ring was precisely dated.

Two types of variables were calculated from the teak microdensity profiles. At first, physical variables commonly used to describe wood quality were calculated at ring level:

- width: ring width (mm)
- m: mean ring density (kg/m^3)
- mi: minimum ring density (kg/m^3)
- ma: maximum ring density (kg/m^3)
- rsd: ring density standard deviation (an indication of the density variability within the ring) (kg/m^3)

Secondly, a set of new variables were computed based on an original ring density model designed to describe the ring structure of teak wood.

2.3 Ring structure modelling and statistical analysis

A four-line segmented linear regression (Sauter et al. 1999) was used to describe the intra-ring density variations as shown in Fig. 1. The decision on the segmentation is based on the location of the breakpoints. This location is automatically chosen by the regression procedure, in order to globally optimize the goodness of fit of the segmented regression. It is necessary to provide an initial set of break points: the first in correspondence with the low density values at the beginning of the ring, the second at the steep change of ring density and the third at the high values at the end of the ring.

As shown in the introduction, the parameters of said model are related to the porosity of teak rings and thus to teak aesthetic value. The model was calculated for all rings of all profiles and the following model-variables were computed:

- dbp1: density of the profile at the first break point (kg/m^3)
- dbp2: density of the profile at the second break point (kg/m^3)
- dbp3: density of the profile at the third break point (kg/m^3)
- pbp1: position along the ring profile of the first break point (mm)
- pbp2: position along the ring profile of the second break point (mm)
- pbp3: position along the ring profile of the third break point (mm)
- slope2: slope of the second segment of the regression line
- slope3: slope of the third segment of the regression line

The segmented model fitted very well the microdensity profiles of the rings until the year 1995. After 1995, due to the lack of opportune thinning, ring width sharply decreased (Fig. 2). The corresponding ring structure was extremely irregular and the microdensity profiles were not able to be correctly described because of inadequate

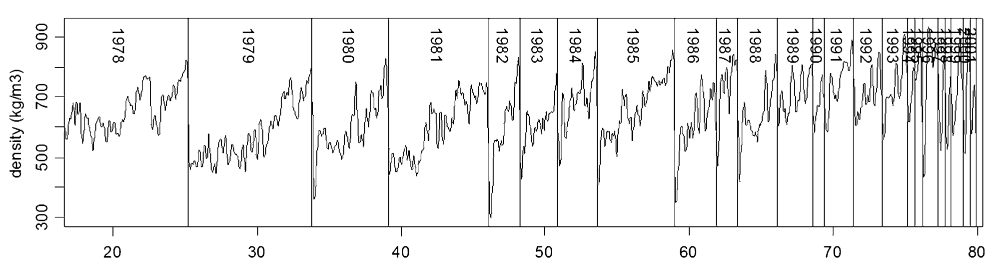

Fig. 2 A typical microdensity profile showing juvenile wood up to ring 1982 and a sharp decrease of ring width due to the lack of opportune thinning

resolution. Therefore, we decided to exclude these rings from the data processing.

One important objective of our work is to study between-provenance variation for ring anatomical structure (from ring porous type to diffuse porous type). But in ring porous trees, ring porosity character develops gradually over time and appears clearly in the mature wood (Zobel and Sprague 1998): there is very little between-tree variation for ring structure in teak juvenile rings. The rings before 1982 have the typical shape of teak juvenile wood according to Bhat (2000) and Bhat et al. (2001) in all trees. Other authors found the transition from juvenile to mature wood after 8–10 years from pith (Kedharnath et al. 1963; Sanwo 1987; Bhat et al. 2001; Kokutse et al. 2010) which also corresponds generally to year 1982 in our sample. Only after 1982 does a typical ring porous structure appear in our trees. For these reasons, we decided to also exclude the rings before 1982 from our analysis (Fig. 2). Therefore, the 1982–1995 rings, which can be taken as representative of the major part of the stem volume, were used to describe the whole stem.

Typical rings were visually selected by anatomical observation and used to construct a porosity index: 31 rings were observed to select 12 typical ring porous rings (rp—abundant and large lumen vessels in the earlywood, followed by an abrupt decrease of vessel lumen area—Fig. 1a), 11 diffuse porous rings (dp—smaller lumen of vessels in the earlywood and very gradual decrease of vessel abundance and lumen area—Fig. 1b), and eight irregular-structure rings (*dp2*), without a clear trend of vessels dimension and vessel distribution changes across the ring; these were classified as an intermediary type.

A discriminant analysis was performed on these selected rings in order to find out the linear combination of the model-variables that best separate the ring porous rings from the two other groups. In the discriminant analysis the factorial groups were the three ring structure groups (rp, dp and dp2), while all the model-variables described above were included as numeric variables. The two linear components best explaining the variance among the three groups were selected. Then, the linear combination of numeric variables best separating the groups was applied to the model-variables of all the rings of all sampled trees and a new variable was computed and called the ring porosity index (model 1).

$$W_{ij} = a_{i1}x_{1j} + a_{i2}x_{2j} + \ldots + a_{in}x_{nj} \tag{1}$$

W_{ij} is the values of the linear discriminant i for the jth ring (ring porosity index); $a_{i[1\ldots n]}$ is the canonical weight of the linear discriminant i for the nth variable and $x_{[1\ldots n]j}$ is the value of the nth variable of the jth ring.

The discriminant analysis was performed with the *discrimin* function of the package "ade4" in R.

Simple correlations (Pearson correlation coefficients) were then calculated among ring variables (classical micro-density variables and ring porosity index).

Afterwards, a two-way analysis of variance was performed including ring and provenance factors as sources of variation for all the microdensity variables and for the ring porosity index, as shown in model 2:

$$Y_{ijr} = \mu + \alpha_i + \beta_j + \gamma_{ij} + +\varepsilon_{ijr} \tag{2}$$

where Y_{ijr} is the observed value of the ring i in the provenance j and replicate r, μ is the overall mean, α_i is the effect due to the ith ring (fixed effect), β_j is the effect due to the jth provenance (random effect), γ_{ij} is the interaction between the ith ring and jth provenance (random effect), ε_{ijr} is the random error.

Finally, the variation among provenances was illustrated in scatterplots, drawn for all the traits (provenance average) versus the annual precipitation of the provenance region as shown in Table 1.

3 Results

The four-line segmented regression generally fitted well the ring microdensity profiles (Fig. 1). In total, 808 rings of 62 trees were analysed. The mean adjusted coefficient of determination of the segmented model was 0.76 (standard deviation=0.21).

Figure 3 shows the results of the discriminant analysis performed on the rings selected to construct the ring porosity index. The rp group (ring porous) is very well separated from both other groups (diffuse porous rings, dp, and the irregular shaped, dp2) along the horizontal axis, that is the first linear discriminant (eigenvalue=0.87). Hence, only the first linear discriminant was used to construct the ring porosity index; Table 3 reports the coefficients (canonical weights) for the standardized (*z*-transformed) variables used to the index computation according to model 1.

The correlation coefficients between all the possible combinations of the ring porosity index and the other ring microdensity variables are shown in Table 4. The correlations were significant, negative and weak for ring width with all microdensity variables and with the ring porosity index. Significant, positive and strong relationships were detected between mean ring density and both minimum and maximum density, as well as between ring density standard deviation and the ring porosity index. The ring porosity index was also negatively and moderately correlated with minimum ring density.

The results of the analysis of variance for all the microdensity variables and the ring porosity index are

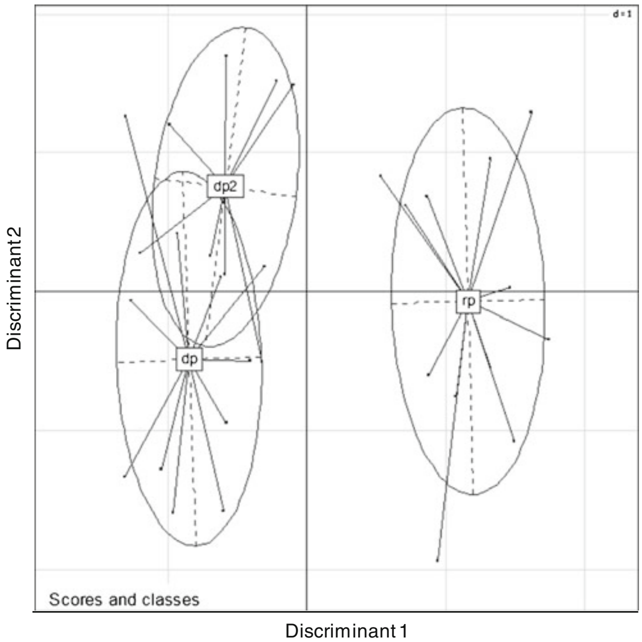

Fig. 3 Results of the discriminant analysis performed on three groups of rings visually selected by anatomical observation (*rp* porous ring; *dp* diffuse porous; *dp2* irregular intermediate structure); data plotted on the first linear discriminant axis (*horizontal*) and second linear discriminant axis (*vertical*). The first linear discriminant axis was used to compute a ring porosity index for each ring of all microdensity profiles

reported in Table 5. Both ring and provenance factors had a highly significant effect on all the variables analysed, except for the provenance factor over the ring width; while the *ring* × *provenance* interaction was never significant. Therefore, the year of ring formation seems to be the key factor to determine ring width, but almost as important as provenance to explain the variation of ring density and ring anatomical structure.

The variation among provenances was represented in scatterplots: trait vs the annual precipitation of the region of origin. Here only the plots for minimum density and ring porosity index are reported (Figs. 4 and 5); the trends were very similar for the other microdensity variables. The provenances 3,047 and 3,021 differ from the others because of their highest mean, minimum and maximum density and their lowest ring porosity index (i.e. diffuse porous rings). On the contrary, provenances 3,048, 3,050 and SG4 differ because of their very low density (both mean, minimum and maximum) and provenance 3,059 because of its low minimum density but not because of mean and maximum density (data not shown); all these provenances were characterized by high ring porosity index (i.e. ring porous), although they do not separate so clearly in Fig. 5.

There is no significant correlation between rainfall of the provenance regions and any of the study traits.

Table 3 Coefficient values (canonical weights of the first linear discriminant) for the computation of the ring porosity index (model 1)

Variable ($x_{[1\ldots n]}$)	Coefficient ($a_{1[1\ldots n]}$)
dbp1	−0.834
dbp2	0.176
dbp3	0.369
pbp1	−0.208
pbp2	0.281
pbp3	−0.530
slope2	0.088
slope3	−0.018

The coefficients apply to *z*-transformed variables

Table 4 Pearson correlation coefficient between all combinations of microdensity variables (width = ring width; m = mean ring density; mi = minimum ring density; ma = maximum ring density; rsd = ring density standard deviation) and ring porosity index

Variable	Width	m	mi	ma	rsd
m	−0.31[c]				
mi	−0.34[c]	0.71[c]			
ma	−0.07[a]	0.76[c]	0.36[c]		
rsd	−0.19[c]	Ns	−0.47[c]	0.37[c]	
index	−0.29[c]	Ns	0.53[c]	0.17[c]	0.79[c]

Ns not significant

[a] Significant at α=0.05

[b] Significant at α=0.01

[c] Significant at α=0.001

4 Discussion and Conclusions

A significant provenance effect was detected for all the microdensity variables except ring width, showing that both wood density variables and ring anatomical structure (as described by the ring porosity index) were influenced by their genetic origin. On the contrary, ring width seemed to be influenced mainly by the year of ring formation.

Studies carried out in the past on the anatomical characteristics of teak wood (Bhat and Priya 2004; Varghese et al. 2000) concentrated on single wood elements (i.e. vessel diameter, fibre length or cell wall thickness), by means of time consuming and laborious measurements. Microdensitometry is an alternative to direct measurement of anatomy. It is quicker and provides a comprehensive and indirect view of wood anatomical features. The segmented model developed in this work describes the anatomical structure of the rings. The parameters of the model effectively distinguish the different ring structures (ring

Table 5 *F* values and significance as results of the analysis of variance including ring and provenance factors and their interaction as sources of variation, calculated for each microdensity variable (width = ring width; m = mean ring density; mi = minimum ring density; ma = maximum ring density; rsd = ring density standard deviation) and for the ring porosity index

Source of variation	Width		m		mi		ma		rsd		Index	
Ring	26.7	a	15.3	a	16.3	a	4.9	a	9.7	a	8.1	a
Provenance	1.3	ns	14.2	a	13.1	a	5.5	a	5	a	5.5	a
Ring × provenance	0.6	ns	0.9	ns	1.0	ns	0.9	ns	0.7	ns	0.8	ns

ns not significant

[a] Significant at α=0.001

and diffuse porous) leading to the development of an efficient ring porosity index. The standard deviation of the ring density profile, firstly and the minimum density of the ring, secondly, are the ring variables best explaining the ring anatomical structure. The lower the minimum density (abundant vessels with large lumen area in the initial part of the ring) and the higher the standard deviation of the ring (strong variation of vessel distribution and of vessel dimension within the ring), the higher the value of the ring porosity index and the more porous is the ring structure.

Ring porosity is one of the causes of the wood colour variation: homogeneous anatomical structure (diffuse porous structure) results in a more uniform wood colour, while high intra-ring variability (ring porous structure) enhances the figure of wood. This is a very important aspect for valuable timber species, such as teak, which are highly appreciated for their aesthetic characteristics.

The veining of teak is known to show geographic (Varghese et al. 2000; Macchioni et al. 2007) and provenance variation (Bhat and Priya 2004), but no provenance trials have been studied for this purpose. In our work, trees from different provenances grown in a replicated experiment showed significant differences in ring structure, demonstrating the importance of provenance on the wood anatomy and therefore on the veining of teak. According to our results, provenances 3,059 and SG4, followed by provenances 3,048, SG1, 3,050 and 3,056 have a ring porous structure and thus most likely a higher aesthetic value.

On the contrary, Varghese et al. (2000) reported the presence of different ecotypes for teak in India, mainly associated to the geographical variation of annual precipitations (very dry, dry, semidry, moist and very moist), and underlined the valued figure of the wood from dry areas. Although they did not find any clear latitude or climate trend for fibre or vessel features, significant differences among sites were observed. In the same way, Thulasidas et al. (2006) described a “darker heartwood with decorative black streaks” in teak grown in dry locations.

Similar results were found by Macchioni et al. (2007): the trees grown under dry climates formed large lumen vessels at the beginning of the vegetation period and small-lumen vessels later. They had a higher heterogeneity of wood density along the ring profile, typical of ring porous rings, if compared to teak rings from wet climates.

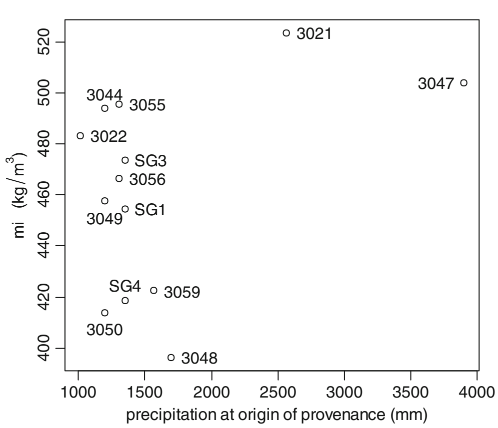

Fig. 4 Scatterplot for the provenance mean value of minimum density (mi) and annual precipitation of provenance origin

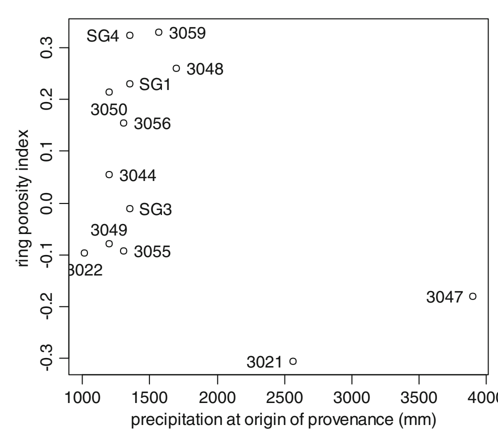

Fig. 5 Scatterplot for the provenance mean value of ring porosity index (index) and annual precipitation of provenance origin

Therefore, we tested the relationship between ring variables and rainfall level at the seed origin of the provenances. No significant correlation was found, but the two provenances from very wet climates were distinguished by low values of ring porosity index (diffuse porous ring). This absence of a relationship could be due to the relatively low variability of rainfall among most provenance regions. Most provenances come from regions with precipitation between 1,000 and 1,700 mm. Only two provenances (3,021 and 3,047) came from a very wet climate (2,565 and 3,900 mm of annual precipitation respectively) and these two provenances distinguished themselves from all the other provenances with low values of the ring porosity index (diffuse porous ring). The variation for ring characteristics among the provenances coming from the dryer regions is also important, nevertheless it is not accounted for by the total annual precipitation of the region of origin. It may be that rainfall at the point of origin is less important than rainfall at the site where the trees are growing. It is also possible that, at least during certain years, water availability at critical times of the growing season is a key factor. Other environmental variables of the region of origin affecting water availability should be investigated like for example the temperature, the atmospheric humidity and the distribution of the rainfall during the growing season.

Water availability during the vegetation period highly influences the cambial activity of teak and, as a consequence, its wood anatomical structure. Priya and Bhat (1999) compared wood formation in irrigated and non-irrigated plants during the vegetation period and found that the typical ring porous structure was lost in the irrigated trees: their growth rings showed a diffuse porosity, decreasing the difference between early- and latewood and making less evident the ring boundary, thus affecting the figure of the wood. These results show that wood anatomy is modified by the variation of water availability. Since the variation of vessel characteristics affects sap conduction, it means that a potential for adaptive phenotypic plasticity could also exist in teak for wood anatomical traits.

Thus, the anatomical structure of teak is affected by the growth conditions, mainly rainfall and water availability, but an influence on the wood density and the ring structure can be also ascribed to tree origin. Our results show that the progenies, composing the provenances of our study, collected in regions of origin with various climate conditions, planted under new climate condition, still have wood characteristics typical of their mother trees: it suggests that these ring characteristics are inherited. This is supported by the fact that, in many species, several basic wood properties, including density, are highly heritable (Zobel and van Buijtenen 1989; Zobel and Jett 1995). Further studies are necessary to estimate the heritability of teak wood density and of linked properties (wood anatomy) in progeny and clonal tests or in areas of natural origin.

Our results suggest that the geographical structure variation found by many authors in the teak natural area could be the result of evolution. However, the hypothesis that geographical variation for water availability may have triggered the selection of phenotypes better adapted to local conditions is not well demonstrated by our results and should be investigated in a specific study. Since at least some of the traits associated to such adaptive phenotypic variation are related to basic wood properties, given that these are known to be moderately to highly heritable, the corresponding phenotypes have been probably transmitted to the offsprings planted in this African provenance trial.

Phenotypic plasticity and genetic adaptation are both mechanisms involved in local adaptation. New studies involving progenies and clones are necessary to estimate the potential for local adaptation to water availability in teak. Progenies are necessary for estimating narrow sense heritability and additive variation, while clones are required for measuring site-related phenotypic plasticity. Such results will provide useful insights for understanding and predicting the response of introduced teak populations to local climate conditions and the final impact on their wood properties and aesthetic value.

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