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Isozyme variation among teak (*Tectona grandis* L.f.) provenances

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Abstract Fourteen enzyme systems were analysed in leaf parenchyma of nine native and introduced populations of teak. These enzyme systems were encoded by 20 putative loci of which 18 were polymorphic. Populations showed a general lack of heterozygosity (average $F_{IS} = 0.11$). On average over the 18 polymorphic loci, the genetic differentiation among provenances varied according to the estimator: 0.09 for G_{ST}, 0.12 for F_{ST} and 0.19 for δ. The cluster analysis showed two main gene pools, the first consisted of the Indian provenances and the second of African, Indonesian and Thai provenances. Genetic distances among populations of the same group were similar, and lower than the genetic distances between populations from different groups. The factorial analysis on genotypes of seedlings also showed the same geographic differentiation into two major groups. The possible natural distribution of teak in Java is discussed.

Key words Allozymes · Genetic differentiation · Isozyme · Polymorphism · *Tectona grandis*

Introduction

Teak, *Tectona grandis* L.f., a member of the *Verbenaceae* family, one of the most economically important tropical timber species, is native to the tropical deciduous forests. Teak is a diploid species (2n = 36) according to Gill et al. (1983). Its natural range may be divided into three disjunct regions (Hedegart 1976): (1) Central and East India, (2) Myanmar, Laos and North West Thailand and (3) Indonesia (especially Central and East Java, and some geographically close islands such as Muna and Betung). The centre of origin of this species is presumed to be in Myanmar (Méniaud 1930), and it has been suggested (Altona 1922) that teak was introduced into Java during the Hindu period, during the VIth-XIVth centuries.

Since the beginning of 19th century the tree has been planted world-wide in the tropical regions of Asia, Africa and Central America (Méniaud 1930; Chollet 1967; Keogh 1979; Dupuy 1990). International provenance trials supported mainly by FAO, DANIDA and CIRAD-Forêt (formerly Centre Technique Forestier Tropical, CTFT) were established extensively in the 1970s in Africa, Central America and South-east Asia (Piot 1977; Egenti 1978; Kaosa-Ard 1986; Keogh 1987), and these have shown an important geographic diversity with respect to quantitiative traits. However, any knowledge that has been acquired on genetic variation using genetic markers to date is poorly understood (Kumaravelu 1979; Verhaegen, unpublished).

The present study therefore focused on the estimation of genetic diversity among stands. Nine teak populations, representing both the three native regions mentioned above (India, Thailand and Indonesia) and artificial habitats (West and East Africa) were analysed. Phylogenetic relationships among provenances and their genetic differentiation were then discussed.

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Materials and methods

Plant material

Eight teak seedlopts (bulked from numerous mother trees) of native and artificial habitats were investigated; these included two West Indian populations (I_1 and I_2) from Karnataka province (the occidental natural range); two Thai stands (T_1 and T_2) from the same locality (the oriental natural range), representing natural forest (T_1) and

plantation (T_2); two Indonesian stands (J_1 and J_2, Central and East Java, respectively): and two stands planted outside the natural range in West (A_1, Ivory Coast) and East (A_2, Tanzania) Africa (Table 1). One additional provenance, Thithimathy Royal Forest (Karnataka, India, I_3), consisting of separated progenies harvested from ten trees, was also available and used for the genetic analysis of isozyme patterns.

Seed germination

Prior to germination teak fruits enclosing one to four seeds each were exposed to 80° ± 1 °C for 48 h in order to break down seed dormancy it was the most efficient of the pre-treatments tested. Seeds germinated within a month in a water-saturated sand media, at 30 °C, under a 16-h photoperiod. Seedlings (about 20 days after cotyledon emergence) were thereafter transferred into greenhouse conditions (minimal temperature 27 °C, natural lighting complemented to a 16-h photoperiod). In most cases, the thermic pre-treatment was efficient to enhance the germination to teak seeds under laboratory conditions. Nevertheless, the germination capacities varied according to the seedlots (from 5% in T_2 to 95% in I_3).

Isozyme technics

The enzyme activities were extracted from young leaves (limb without principal and secondary midribs) harvested from at least 2-month-old seedlings. The leaf samples collected were immediately ground at 5 °C in a mortar containing the extraction buffer (360 µl for 200 mg plant material), which was a sodium tetraborate buffer (50 m*M*, pH 8.3) supplemented with 0.1% dithiothreitol, 2.0% polyvinyl pyrrolidone 40,000, 1.0% polyethyleneglycol 20,000, 1.0% bovine serum albumin, 0.25 *M* ascorbic acid, 0.2 m*M* pyridoxal-5'-phosphate, 0.4 m*M* nicotinamide adenine dinucleotide, 0.3 m*M* nicotinamide adenine dinucleotide phosphate, 0.45 *M* sodium thioglycolate and 0.14 *M* sucrose. The homogenates were centrifuged at 15,000 *g* for 20 min at 4 °C. The electrophoretic migration took place at 5° ± 1 °C in a vertical polyacrylamide gel under an electric field of 12 $V \cdot cm^{-1}$ for 4.5–5 h. The electrode and gel buffer was Tris (90 m*M*) borate (90 m*M*), ethylenediamine tetraacetic acid disodium salt (2.5 m*M*), pH 8.38. Standard staining procedures were adapted with some minor modifications from Vallejos (1983). Cheliak and Pitel (1986), Pasteur et al. (1987) and Wendel and Weeden (1989) except for carboxyl esterase, which was revealed in a barbital buffer (50 m*M*, pH 8.2) containing indoxyl acetate (1.1 m*M* previously dissolved in acetone), and cupric acetate (0.1 m*M*).

Of the 69 enzyme activities tested (some were tested with various substrates and staining procedures), the following 14 were finally retained because of reproducible patterns and of a possible genetic analysis of patterns in each individual: alanine aminopeptidase (E.C. 3.4.11.1) (AAP), aspartate amino transferase (E.C. 2.6.1.1.) (AAT), acidic phosphatase (E.C. 3.1.3.2) (ACP), alcohol dehydrogenase (E.C. 1.1.1.1) (ADH), diaphorase (E.C. 1.6.4.3) (DIA), endopeptidase (E.C. 3.4.-.-) (ENDO), carboxyl esterase (E.C. 3.1.1.-) (EST), fluorescent β-D-glucosidase (E.C. 3.2.1.21) (β-GLU), glycerate-2 dehydrogenase (E.C. 1.1.1.29) (G_2DH), leucine aminopeptidase (E.C. 3.4.11.1) (LAP), lactate dehydrogenase (E.C. 1.1.1.27) (LDH), nicotinamide adenine dinucleotide dehydrogenase (E.C. 1.6.99.3) (NADH-DH), peroxidase (E.C. 1.11.1.7) (PER) and superoxide dismutase (E.C. 1.15.1.1) (SOD).

Data processing

Inheritance of each enzymatic system pattern was assesssed in the ten half-sib progenies. The genotypes of all seedlings from each stand, grown under greenhouse conditions, were then deduced from the banding patterns observed for each enzyme system (Kertadikara and Prat 1995).

Genetic linkage between 2 loci can be detected when gametes produced by an individual mother heterozygous at these both loci are identifiable in its progenies. In half-sib families, the genotype of the maternal gametes can be determined when pollen gametes bring an allele not present in the mother tree (locus having at least 3 alleles), or when individual progenies are homozygous. The random association of alleles at different loci was tested (χ^2 test) in maternal gametes of a known genotype; this tested linkage between considered loci.

The genetic structure among individual populations was estimated using F-statistics (Wright 1965), G-statistics (Nei 1973), the amount of genetic differentiation of the demes and the level of differentiation among demes, δ (Gregorius 1985). The similarity among single populations was measured by estimating the Nei unbiased genetic distances (Nei 1978) and Gregorius genetic distance (Gregorius 1985). Dendrograms produced by cluster analysis according to the Wagner distance method (Farris 1972) or to the unweighted pair-group method with arithmetic averaging (UPGMA) (Sneath and Sokal 1973) were thereafter drawn to represent the phylogenetic relationships among individual populations. These parameters were assessed using the Biosys-1 package (Swofford and Selander 1981). In order to complete these approaches, multivariate analyses (factorial analysis) based on the presence or absence of each detected genotype or allele at each locus was also conducted. The variable in the genotypic analysis was denoted as 1 only when the corresponding locus genotype was that of the considered individual; under other conditions, it was designated 0. In the allelic analysis, the variable was denoted 2, 1 or 0 when the allele considered was observed in a single individual, in the homozygous condition, in the heterozygous condition or not observed, respectively.

Results

Isozyme patterns

Eighteen isozyme polymorphic loci (*Aap*, *Aat-b*, *Aat-c*, *Acp-b*, *Adh*, *Dia-a*, *Dia-b*, *Endo*, *Est*, *β-Glu*, *G_2dh-a*, *Lap*,

Table 1 Geographic origin of *Tectona grandis* provenances

Provenance	Country	Longitude	Latitude	Elevation	Number of seedlings
I_1 Sakrebail Royal Forest Seed production area	India	75° 29′ E	13° 48′ N	600 m	9
I_2 Virnoli Seed production area	India	74° 37′ E	15° 12′ N	600 m	55
I_3 Thithimathy Royal Forest	India	67° 00′ E	12°15′ N	850 m	263
J_1 Kandangan	Indonesia	110° E	7° 00′ S	300 m	18
J_2 Saradan	Indonesia	111° E	7° 30′ S	320 m	10
T_1 Tam Bah Thai Mae Huat Natural Forest	Thailand	99° 55′ E	18° 40′ N	350 m	16
T_2 Mae Huat Seed production area	Thailand	99° 55′ E	18° 40′ N	350 m	3
A_1 Kokondekro	Ivory Coast	5° 02′ W	7° 38′ N	280 m	97
A_2 Tanzania[a]	Tanzania	37° E	7° S		82

[a] No more data available

Table 2 Genetic diversity among *Tectona grandis* provenances analysed by F-statistics, G-statistics and δ at 18 polymorphic loci

Locus	F_{IT}	F_{IS}	F_{ST}	H_T	H_S	G_{ST}	δ
Aap	0.129	0.057	0.076	0.601	0.589	0.020	0.203
Aat-b	0.647	0.513	0.275	0.655	0.443	0.324	0.404
Aat-c	−0.042	−0.142	0.088	0.311	0.297	0.044	0.148
Acp-b	0.430	0.332	0.146	0.688	0.627	0.089	0.259
Adh	0.213	0.065	0.158	0.184	0.178	0.032	0.193
Dia-a	0.517	0.478	0.075	0.499	0.480	0.037	0.158
Dia-b	0.443	0.344	0.151	0.521	0.462	0.112	0.227
Endo	0.147	0.055	0.097	0.524	0.493	0.059	0.211
Est	0.192	0.061	0.139	0.679	0.602	0.113	0.319
β-Glu	−0.027	−0.065	0.036	0.076	0.074	0.017	0.028
G_2dh-a	0.016	−0.185	0.170	0.612	0.492	0.195	0.293
Lap	0.395	0.345	0.076	0.111	0.106	0.043	0.094
Ldh	0.460	0.197	0.328	0.546	0.413	0.243	0.329
Nadh-dh	−0.042	−0.093	0.046	0.174	0.162	0.071	0.079
Per	−0.073	−0.131	0.051	0.240	0.235	0.023	0.091
Sod-a	−0.140	−0.189	0.042	0.249	0.239	0.039	0.070
Sod-b	0.451	0.401	0.084	0.494	0.458	0.072	0.135
Sod-c	0.067	−0.050	0.112	0.445	0.430	0.034	0.137
Mean	0.210	0.111	0.119	0.423	0.377	0.087	0.188

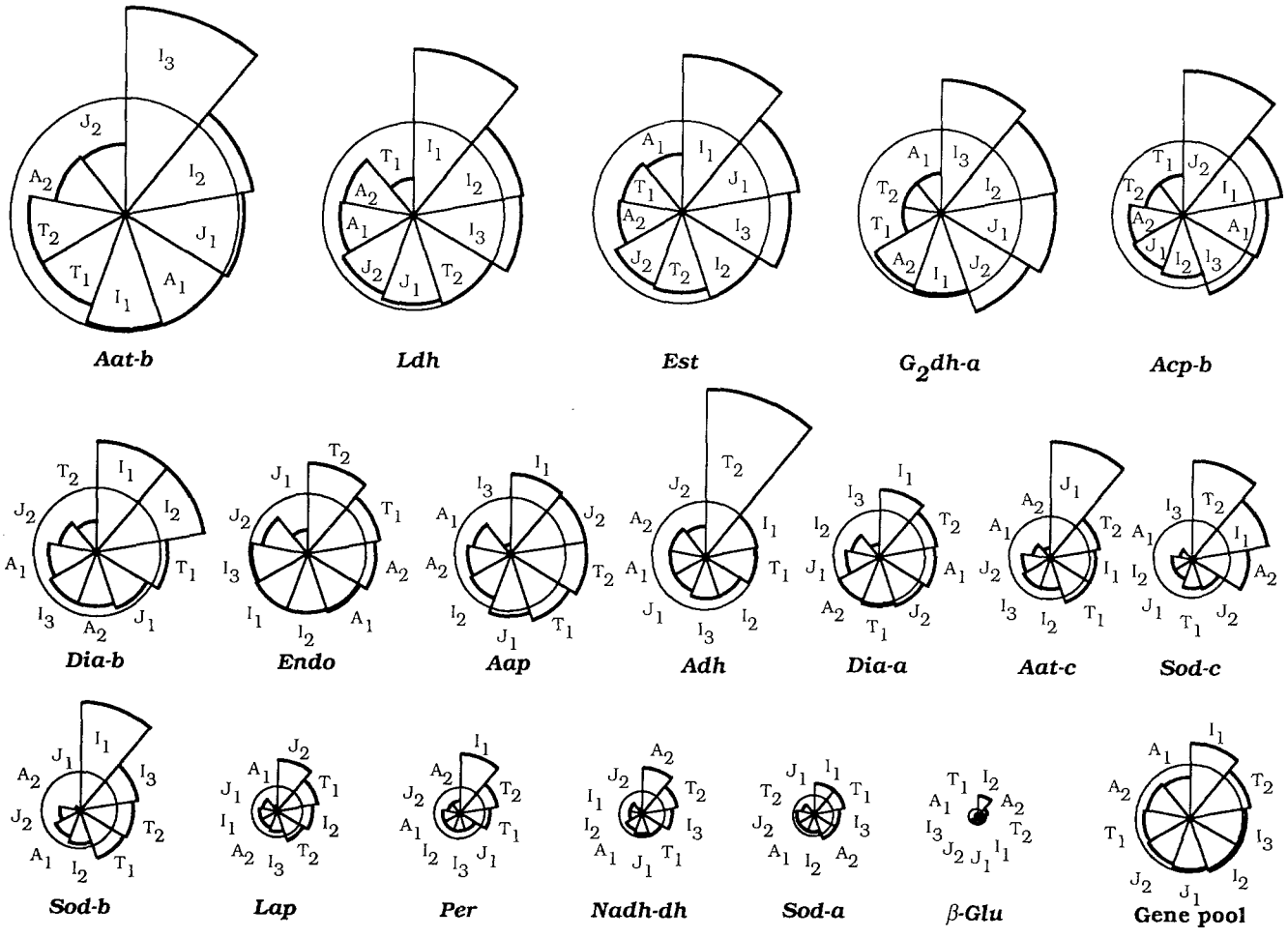
Fig. 1 Genetic differentiation among provenances of *Tectona grandis* according to Gregorius (1985) at the 18 polymorphic loci analysed

Ldh, *Nadh-dh*, *Per*, *Sod-a*, *Sod-b* and *Sod-c*) encoding 14 enzyme systems were therefore scored. Two monomorphic loci were also noticed: *Aat-a* and *Sod-d*. Eighty alleles were scored in the nine populations of teak at the 18 polymorphic loci.

The genotypes of more than 20 maternal gametes could be identified in different half-sib families for the following combinations of loci: *Aap-Acp-b*, *Aap-Endo*, *Aap-Est*, *Aap-Ldh*, *Acp-b-Endo*, *Acp-b-Est*, *Acp-b-Ldh*, *Acp-b-Sod-b*, *Dia-a-Endo*, *Dia-a-Sod-c*, *Endo-Est*, *Endo-Ldh*, *Endo-Sod-b*, *Est-Ldh*. Alleles from the loci considered were randomly associated in each case. No linkage tendency was detected.

Genetic diversity among provenances

The geometric average of the fixation indices in the provenances (F_{IS}) and in the total population (F_{IT}) calculated over 18 polymorphic loci were positive and 0.11 and 0.21, respectively. The differentiation between provenances, assessed by F_{ST}, gave an average of 12%, ranging across the loci from 3.6% (*β-Glu*) to 33% (*Ldh*). This showed an important differentiation at some loci, mainly *Aat-b* and *Ldh*. While other loci were less differentiated (Table 2). The results suggest that the teak



provenances were structured in several sub-populations of different geographic origin.

The average gene diversity (Table 2) in the total population ($H_T = 0.42$) was greater than that of within sub-populations ($H_S = 0.38$). Among provenance relative gene diversity (G_{ST}) was about 9%; on average, 91% of the gene diversity resided within a population. The G_{ST} values ranged across the loci from 1.7% (*β-Glu*) to 32% (*Aat-b*), confirming the previous result obtained by Wright's F-statistics method; both the *Ldh* and *Aat-b* loci were the most differentiated.

Similar results were found using levels of differentiaiton among provenances δ. Variation was also observed with respect to locus, from 2.8% (*β-Glu*) to 40% (*Aat-b*), with an average of 19% over 18 loci (Table 2). The *Ldh* and *Aat-b* were once again the most differentiated loci. A relatively high amount of genetic differentiation of populations was noticed (Fig. 1), ranging across the populations from 14.3% (African provenance A_1) to 26.0% (Indian provenance I_1) The Indian provenances (especially I_1) and Thai provenance T_2 were therefore the most differentiated provenances.

Allelic frequencies were significantly different depending upon the provenance ($\chi^2 = 58.0^{***}$). Some alleles, those at high frequencies, particularly DIA-b_2 and DIA-b_3, EST_3 and EST_5, AAT-b_2 and AAT-b_5, G_2DH-a_1 and G_2DH-a_3 and LDH_2 and LDH_4, could be used to characterise the geographic origins of populations. Those alleles clearly separated the Indian provenances from the African and Indonesian provenances.

While the Nei unbiased genetic distances among individual populations were relatively smaller than those of Gregorius (Table 3), both could be interpreted similarly. The values ranged from 0.02 to 0.24 and from 0.11 to 0.37, respectively. Within Indian populations, the Gregorius distances ranged from 0.11 to 0.22. Meanwhile, greater distances (from 0.25 to 0.37) were observed between the group of Indian provenances on the one hand and the group of Indonesian, Thai and African provenances on the other hand. Among the provenances from this second group, Gregorius genetic distances ranged from 0.13 to 0.23, the same range as among the Indian provenances. Low genetic distances separated the populations that were close geographically. The Indian populations were genetically distinct with respect to the rest of populations.

The UPGMA dendrogram using Nei's unbiased distance showed the same clustering of provenances as that obtained by the Wagner procedure using Gregorius distances (Fig. 2). The phylogenetic trees revealed two major groups, the first one consisting of the three Indian provenances, while the second one consisted of the African, Thai and Indonesian provenances. The general

Table 3 Genetic distances among *Tectona grandis* provenances [unbiased Nei (1978) genetic distance above diagonal, Gregorius (1985) genetic distance below diagonal] based on 18 polymorphic loci

Provenance	I_1	I_2	I_3	J_1	J_2	T_1	T_2	A_1	A_2
I_1 Sakrebail	–	0.054	0.082	0.202	0.167	0.186	0.245	0.175	0.173
I_2 Virnoli	0.191	–	0.024	0.182	0.153	0.119	0.158	0.137	0.134
I_3 Thithimathy	0.218	0.111	–	0.196	0.184	0.119	0.161	0.151	0.150
J_1 Kandangan	0.314	0.293	0.290	–	0.051	0.074	0.085	0.041	0.038
J_2 Saradan	0.291	0.286	0.308	0.162	–	0.074	0.086	0.053	0.051
T_1 Tam Bah Thai	0.339	0.261	0.218	0.222	0.216	–	0.046	0.058	0.042
T_2 Mae Huat	0.369	0.302	0.246	0.222	0.230	0.167	–	0.073	0.076
A_1 Kokondekro	0.283	0.247	0.259	0.154	0.156	0.188	0.215	–	0.029
A_2 Tanzania	0.310	0.254	0.269	0.152	0.162	0.165	0.205	0.128	–

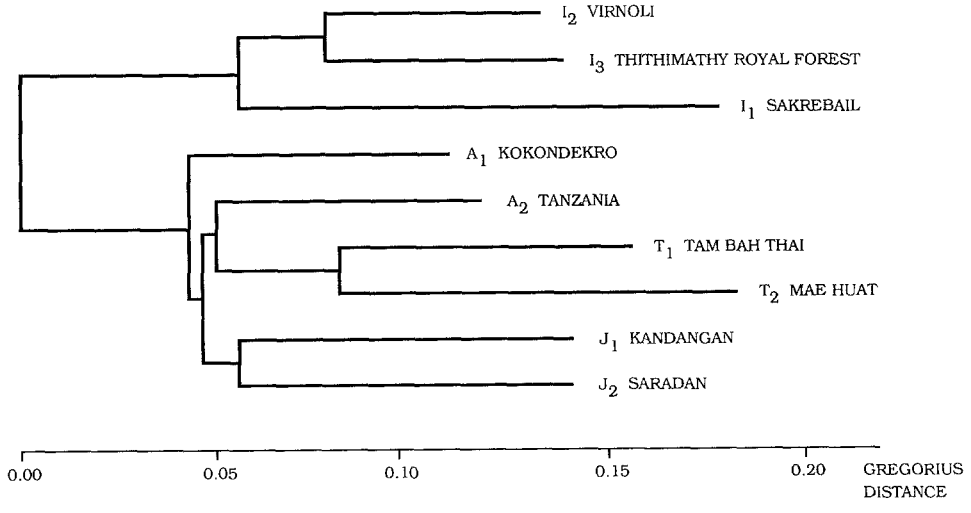


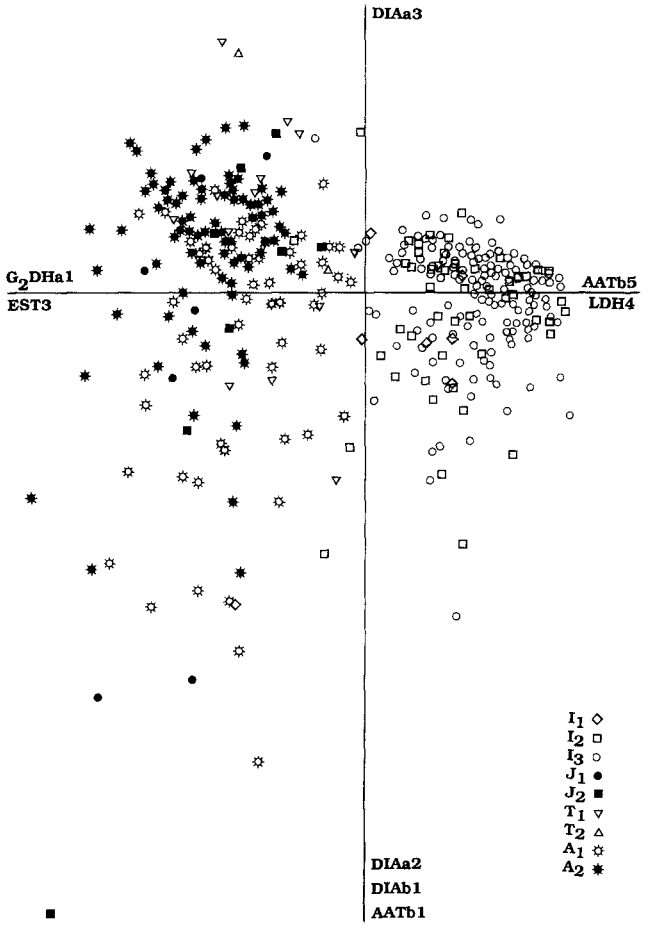
Fig. 2 Relationships among *Tectona grandis* provenances according to the Wagner procedure applied to the Gregorius genetic distance based on 18 polymorphic loci (cophenetic correlation: 0.94)

tendency inside each group was that geographically close provenances clustered together.

Multivariate analysis based either on genotypes or alleles present revealed very similar trends of geographic genetic variation. Only that obtained from the alleles present (70 variables) at 15 loci (*β-Glu*, *Per* and *Acp-b* loci were excluded because of low variation) is shown (Fig. 3). Individual seedlings from each population were then plotted according to the first and second axis (8.3% and 4.3% of inertia, respectively). The first axis was mainly determined by major alleles (frequency > 0.5 in at least one group of provenances): AAT-b_5 and LDH_4 in opposition to G_2DH-a_1 and EST_3. The second axis included less abundant alleles (frequency > 0.1). Provenances were differentiated with respect to both axes (Table 4). Indian populations were significantly different to all other provenaces in the first axis, while in the second axis Thai and Tanzanian provenances were significantly different from the rest of populations.

The separation between the Indian group and the Indonesian, Thai and African group was observed in each analysis, both at the provenance level as well as at the individual level.

Fig. 3 Factorial analysis based on allele borne by seedlings at 15 polymorphic loci (70 alleles) in nine *Tectona grandis* provenances, axes 1 (8.3% of inertia) and 2 (4.3% of inertia)



Discussion

Differentiation among populations

Regardless of the different models used, almost all of the results were similar, indicating that our teak provenances showed a large gene diversity ($H_T = 0.423$, including both monomorphic and polymorphic loci). This compares favourably with the results of Hamrick and Loveless (1986) and the reviews by Hamrick et al. (1992) or by Loveless (1992) for tropical species. These researchers stated that most of the gene diversity resided within the population (about 90%), and only a small fraction (10%) was therefore among populations, which is what we observed in the present study on teak.

Dominant species (as teak) in wide stands and with a large range, such as *Fagus sylvatica* (Comps et al. 1990), the *Q. petraea* complex (Zanetto et al. 1993), broad-leave tree species or *Pseudotsuga menziesii* (Li and Adams 1989), showed little genetic variation among stands (0.05–0.10), especially stands within the same region. Provenances of *Tectona grandis* appeared rather more differentiated. However, greater genetic differentiation (G_{ST} or F_{ST} about 20%) was observed in species having a wide and disjunct (at least partially) natural distribution, such as *Alnus glutinosa* (Prat et al. 1992) and African acacia, *Faidherbia albida* (Joly et al 1992). In teak, the large genetic differentiation comes mainly from the subdivision of the natural range into separated areas. The separation of the Indian and Indonesian-Thai-African groups was obvious from the different analysis (genetic distance, dendrogram, multivariate analysis). Allelic frequencies of some loci (especially *Aat-b* and *Ldh*) for which there was no evidence of linkage, also differed significantly among the two groups. This differentiation cannot be related to latitude since the Thai-Indonesian group included low and high latitude provenances.

The situation of the African populations is ambiguous on the basis of their introduction history. They came mostly from India, so that any genetic relatedness was expected to be in the direction of the Indian populations rather than to Thai or Indonesian populations. Nevertheless, several authors (Méniaud 1930; Chollet 1967; Egenti 1978; Madoffe and Maghembe 1988) have advocated that the African populations consist in fact of mixtures of several seed origins (India, Myanmar, Java and Thailand). Assuming that there was no genetic drift and considering international provenance trials that have shown that the Indian provenances were generally not adapted in African tropical conditions (usually high mortality: Delaunay 1977; Egenti 1978), it can be argued that African provenances became close to the Thai-Indonesia group by selection against Indian material, despite the fact that this source consisted probably of the major introductions.

Table 4 Characteristics of major axes of factor analysis based on allele presence at 15 polymorphic loci (70 recoreded alleles) and variation among provenances according to these axes, tested by variance analysis and multiple range test (probability 0.95) according to Scheffe (1953)

Axis	Variation (%)	Major variables (alleles)	Between/within provenance variance	Provenance range
1	8.34	(+) AAT-b_5, LDH_4 (−) G_2DHa_1, EST_3	268.4***	$J_1\ A_2\ J_2\ A_1\ T_1\ T_2\ I_1\ I_2\ I_3$
2	4.31	(+) DIA-a_3 (−) AAT-b_1, DIA-a_2, DIA-b_1	6.7***	$J_1\ I_1\ J_2\ A_1\ I_2\ I_3\ A_2\ T_1\ T_2$
3	3.44	(+) G_2DH-a_2 (−) ADH_3, ADH_5, LDH_1	3.7***	$T_2\ T_1\ A_2\ I_3\ I_2\ J_1\ A_1\ J_2\ I_1$
4	3.27	(+) DIA-a_1 (−) DIA-a_2, NADH-DH_2	5.0***	$I_1\ J_1\ I_2\ A_2\ J_2\ I_3\ A_1\ T_1\ T_2$
5	3.08	(+) AAT-b_3, EST_4 (−) G_2DH-a_2	5.4***	$A_1\ I_3\ A_2\ I_2\ J_1\ T_2\ J_2\ T_1\ I_1$

*** Significant at the 0.001 level

Historical and palaeobiogeographical considerations on teak dispersal in Asia

The present analysis obviously indicates genetically based variation between the Indian provenances and all the others. This supports the hypothesis that only limited gene flows have occurred between groups isolated geographically for a long time. The current distribution and variation pattern of teak populations can be explained by considering both historical as well as ecological factors.

The hypothesis of teak distribution in Java resulting from human activities and its intorduction from India about 700–1500 years ago (Altona 1922) is not supported by our results. Teak possesses a long life-span, assuming a generation replacement time of about 100 years, thus few successive generations have undergone selective stabilisation since the variation patterns have been established. This relatively rapid differentiation is not probable, particularly in the case of genetic markers (isozyme), these being a priori neutral in an evolutionary sense.

Besides, palaeobiogeographical and climatic considerations during the Quaternary Period in southeast Asia have allowed researchers to reconstruct the putative migration of teak during the past 20,000 years. The Pleistocene, characterised by dramatic alternations between glacial and interglacial periods, had a major impact on climate changes through the interaction of variations in temperature, rainfall and topography (see level). These factors were crucial with respect to the extent of vegetation changes in Southeast Asia (Flenley 1979). Indications of a temperature decline in mainland Asia have been found (Walker 1986) and also of, climate dryness, there is also evidence of a larger regression of tropical evergreen forest in India (Singh 1963) than that nowadays. If we take these data into consideration it can be believed that teak was eliminated in nearly all parts of its mainland natural range, which was apparently more widespread than that nowadays, leaving behind a disjunct present range in mainland Asia that was relict-derived from ancestral populations that "escaped" and persisted, as a glacial refuge.

Meanwhile, glaciation resulted in a decreased ocean volume, causing a sea level decline of about 160 m (Gascoyne et al. 1979) to 120 m (Hopkins 1982). This permitted a connection to be made between the mainland and the islands by the land-bridges (Van Steenis 1962). The late Pleistocene land area can be estimated simply by tracing the 120-m bathymetric line (Heaney 1991). It is imaginable that this dry land, which existed about 18,000 years ago, allowed all living things, including teak, to undergo their possible dispersal from the mainland to the islands in several but small distances following the Pleistocene rivers. The affinities between the Asiatic animals and vegetation when compared to those of the Indo-Malayan region support this idea. Furthermore, being dispersed mainly by water (hydrochory), teak fruit has morphologically some advantages under these conditions: it is a drupe with up to four seeds, one in each lobe, surrounded by a hard outer hairy bark, wrapped by a thin impervious layer and thus adapted to a long migration.

The establishment and success of species implementation in a new habitat depend on edaphic and climatic conditions. In mainland Asia teak is typically a monsoon forest species, adapted to a dry and seasonal climate. Surprisingly, this is also the same situation in the Indonesian archipelago, where teak is exclusively found in the monsoon regions, in the centre and east of Java and in neighbouring small islands.

The hypothetical Pleistocene map of climatic conditions of that region presented by Heaney (1991) shows evidence of an extension of the current area of seasonal forest, as the evaporation and the moisture content of the monsoon winds decreased because of increased land area. Current seasonal forests are confined to the lesser Sunda Islands, eastern Java and south-eastern

Kalimantan, while Pleistocene seasonal forests corresponded probably to the corridor of low rainfall passing through the centre of the Sunda shelf, extending in an arc from southern Thailand to eastern Java (Morley and Flenley 1987). The pattern of teak dispersal was probably continuous from its origin centre somewhere in Myanmar (Méniaud 1930) to Java. It can then be understood that the current disjunct presence of teak in Java resulted from very specific mechanisms of adaptation to the climatic and edaphic conditions. Thus, according to the palaeogeographical and palaeoclimatic data, the natural migration of teak to eastern Java was possible from the Myanmar or Thailand areas during Pleistocene. However, palynologycal data cannot confirm this hypothesis since teak pollen has never been observed in sediments. Human activities are not required to explain the present distribution of teak in Indonesia, but human migration might occur simultaneously.

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