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Full Length Research Paper

Genetic diversity of *Tamarindus indica* populations: Any clues on the origin from its current distribution?

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Tamarindus indica **is a domesticated species of high economic value for the Sahel region. Despite this importance, very few data is available on its diversity as well as its structure leading to controversial discussions on its origin. Thus it is questionable whether the knowledge of its genetic diversity and organisation may help in identifying the area of its origin. We have studied 10 populations using markers RAPDs with the seeds collected from Asia (India and Thailand), Africa (Burkina Faso, Senegal, Kenya and Tanzania), from three islands (Madagascar, Réunion and Guadeloupe). The results showed that *T. indica* has a high intra population genetic variability with a higher value obtained in the population from Cameroon. This high intra-population variability did not allow us to determinate the origin of the species. However, if we take into account the paleontological and anthropological results, we can assume that *T. indica* has an African origin.**

Key words: *Tamarindus indica*, RAPDs markers, genetic diversity origin.

INTRODUCTION

Human migrations and/or exchanges have promoted the worldwide distribution of numerous plant species, such as wheats, rice, maize, potato, and citrus (Brush et al., 1995; Hamon et al., 1999; Nicolisi et al., 2000). Selection has produced specialized phenotypes with genetic differentiation between cultivated forms and their wild relatives. The organization of the genetic diversity of these widespread domesticated plants has been studied and their centres of origin identified in many cases (FAO, 1996). For tree species of lesser current economic importance little information is available and doubts remain regarding the area of origin of some widespread species. This knowledge is of importance for developing efficient *in situ* conservation strategies (Chevallier 1999).

Tamarindus indica is widely distributed in dry parts of Africa and tropical Asia and has been recently introduced into South America, as well as into the Antilles (Guadeloupe) and the Indian Ocean (La Réunion). The periods of these introductions are still unknown and the precise origin of this species is still a subject of controversy (Lefévre, 1971; El-Siddig et al., 1999; Grollier et al., 1998) claimed that it originated in Africa and was introduced into India at an early date, whereas Wunderlin (1998) and Poupon and Chauvin (1983) assumed that its origin is in Asia particularly in India, because of its appelation "Tamar hindi" which when translated means "Indian date" and owing to the fact that Marco Polo in his writings quotes its presence into 1298 and the boudhists sources make noted it 650 years AV J.C.

The spatial distribution of genetic diversity could yield clues to resolve these uncertainties. Introduction events are often associated with a population bottleneck, which should reduce genetic diversity (Citation). The short time elapsed since introductions should not have been suffici-

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ent for mutation to counter such reduction in diversity (Citation). The diversity in an area of introduction should thus be a subset of initial diversity (Citation).

The main objectives of this study were i) to estimate the genetic diversity of *T. indica* and ii) to evaluate whether patterns in the organization of this diversity can provide clues as to the area of origin of the species. In order to address these questions we assessed the genetic diversity of 10 populations of *T. indica*, distributed over its range with Random Amplified Polymorphic DNA (RAPD) markers, which have proved useful for estimating genetic diversity especially for previously unstudied taxa when DNA sequence information are not available (Williams et al., 1990). RAPD analysis has been widely used in assessing the genetic diversity of populations of a large number of trees, including tropical species (Bekessy et al., 2002; Cardoso et al., 1998; Dawson and Powell, 1999; Degen et al., 2001; Gillies et al., 1997; Heaton et al., 1999; Lee et al., 2002; Lowe et al., 2000).

MATERIALS AND METHODS

Knowledge on *T. Indica*

T. indica L. is a semi-evergreen tree which can reach up to 20 m in height. It is a member of the family Fabaceae (Leguminosae), which is the third largest family of flowering plants with 700 genera and approximately 17,000 species (Chant, 1993). It belongs to the subfamily Caesalpinioideae, which can be divided into five to nine tribes or groups of genera based on the morphological characters. In the Bentham's classification (Pettigrew and Watson, 1977), tamarind belongs to the tribe of the Amherstieae Benth. According to Léonard (1957), the Amherstieae comprises 25 genera in total, 21 in tropical Africa, two in tropical America and two in Asia. There are only three relic Afro-Asiatic genera within the group, namely *Humboldtia*, *Tamarindus* and *Amherstia*. Both *Tamarindus* and *Amherstia* are more derived, with zygomorphic and showy flowers and stamen filaments connate in a sheath, but have many differences in the floral structure, leaves, fruits and seeds. These genera are isolated from each other and from the main part of the tribe, centred in western Africa (Polhill and Raven, 1981). *Tamarindus* is said to have some resemblance to *Heterostemon* Desf. from the upper Amazon region of South America. No other tree bearing any resemblance to tamarind has been reported in other countries (Dassanayake and Clayton, 1999). The genus *Tamarindus* contains only one species (monotypic genus). It is a diploid species with a chromosome number of $x = 12$ and $2n = 24$ (Purseglove, 1987; El-Siddig et al., 1999).

Plant material and DNA extraction

Seeds were collected from 10 trees (Guadeloupe) to 30 trees (Kodiena, Burkina Faso) in eight natural or naturalised plantations and two planted stands of *T. indica* covering a large part of the current range of the species (Table 1). For the populations of Cameroon, India and Senegal the number of trees was not specified by the seed centres.

The seeds were allowed to germinate in polycarbonate boxes containing sand and young seedlings were kept in an incubator at 37°C. Total DNA was extracted from 150 mg of foliar tissues from fifteen-day-old seedlings following the protocol of Bousquet et al. (1990). The integrity of the DNA was estimated on agarose gels and the quantity was determined using a fluorimeter DNA was then diluted in sterile water to a concentration of 5 ng/µl for use in amplification reactions.

RAPD analyses

Fifteen primers were screened to identify suitable primers for RAPD analysis, using five individual samples from different provenances. Eight primers able to detect distinct, clearly resolved and polymorphic amplified products were selected for further analysis.

PCR was carried out in a final volume of 25 µl containing 10 mM Tris (pH 8.0), 50 mM KCl, 2 mM $MgCl_2$, 0.1 mM of each dNTP, 0.56 µM of primer, and 1 unit of Taq DNA polymerase. Amplification of RAPDs was performed on a Perkin-Elmer thermocycler using the following PCR conditions: an initial denaturation step at 94°C for 4 min, followed by 45 cycles each at 94°C for 1 min, 36°C for 1 min, 72°C for 2 min and a final extension step at 72°C for 2 min. Negative controls, in which DNA was omitted, were included in each run. Amplification products were separated by electrophoresis on 1.8% agarose gels run in 1X TBE (Tris-Borate-EDTA) buffer, stained with ethidium bromide, visualised and photographed under UV light.

Scoring of bands and statistical analysis

Amplified bands were scored present (1) or absent (0) regardless of band intensities. Ambiguous data were scored as missing data. We analysed the data on three levels of comparison: among individuals, among populations and among areas.

Ressemblances/differences among individuals

The Sokal and Michener index of similarity S (Sokal and Sneath, 1963) was calculated between all individuals, using the software NTSYS-PC (Rohlf, 1993). The value of this index varies between 0 (two individuals not having any common marker) to 1 (two individuals showing identical banding patterns). The matrix of similarities allowed us to calculate the matrix of genetic distances (1-S). A neighbor-joining (NJ) dendrogram was then constructed from these distances using the software DARwin 3.6 (Perrier et al., 1999). We performed a first analysis in order to quantify genetic variability within the potential native range of *T. indica*, and then added planted individuals and individuals from populations of recent introduction.

Quantification and comparison of population diversity

The Shannon index ($H_S=-\sum p_i \ln p_i$) and Nei's index ($H=n(1-\sum p_i^2)/n-1$) where p_i (in both indices) is the frequency of the *i*th RAPD band, as well as the percentage of polymorphic loci (P) at the 0.99 criterion were calculated for each population using Popgen 1.32 (Yeh and Boyle, 1997). Calculation of P is a heuristic approximation for these dominant markers. It is not known whether bands at a particular level correspond to a single locus. Furthermore, only two "alleles" are possible, 'present' and 'absent'. The population genetic structure F_{ST} was computed using AFLP-SURV 1.0 (Vekemans, 2002) following Lynch and Milligan (1994) instead of Φ_{ST} normally applied during AFLP data analysis.

Comparison among areas

To examine differences among areas (East Africa, West Africa, Cameroon, Réunion and Guadeloupe) we grouped individuals with-

Table 1. *T. indica* samples studied for RAPD analysis. *N* denotes the sample size for seeds and *Nb* denotes the sample size of female donor trees of each population.

Country	Population name	Population type	Nb trees	N seeds
Burkina Faso	Kodiena	Natural	30	18
Cameroon	Maroua	Natural	-	16
Kenya	Gédé	Natural	25	16
Senegal	Pamene	Natural	-	18
Tanzania	M'tandika	Natural	22	18
Guadeloupe	Mahaudière	Planted	10	21
India	Dehra Dun	Natural	-	24
Madagascar	Anarafaly	Natural	15	22
Réunion	Etang sale	Natural	16	21
Thailand	Bangkok	Planted	10	12

in each area as an entity and calculated distances of Nei using the software AFLP-SURV 1.0 (Vekemans, 2002). Robustness of the nodes was evaluated by bootstrap (2000 replicates). We used the Neighbor and Consense procedures of the Phylip95 software package (Felsenstein, 1993) to construct the dendrogram and infer boostrap confidence on tree branches.

RESULTS

Intra-population genetic diversity

The eight primers used to screen RAPD diversity of *T. indica* populations generated 58 polymorphic amplification fragments across the whole sample. (Table 2) lists the polymorphic primers, their sequences and the number of polymorphic markers found in the 10 populations (Table 3). We obtained 5 to 10 fragments per amplification with an average of 7.25. Marker 1 is fixed in Guadeloupe, polymorphic in Thailand and India and completely absent from the other populations (Figure 1). The percenttage of polymorphic loci ranged from 39.7% for Thailand to 77.6% for Cameroon with a mean of 69.3 for the African populations. The average within-population diversity was 0.28 and 0.31, respectively, over all populations and the African populations.

Inter-population genetic diversity

The dendrogram of individuals from populations of the potential native range (Figure 2) exhibits three groups: the first group includes the eastern African populations along with the populations from Madagascar and from India, the second group comprises the western African populations and the individuals from Cameroon form a third group (Figure 2). The same analysis carried out with only the five African populations, groups the Cameroonian individuals in a cluster with those from West Africa; Kenyan and Tanzanian individuals form two other groups (Figure 3). The among-populations, genetic diversity was 0.09 for these five populations with F_{ST} = 0.23, highly significant ($P < 0.001$).

Table 2. Polymorphic primers and number of polymorphic markers obtained.

Name of primer	Sequence of primer (5' to 3')	No. of polymorphic markers
OPA-A09	GGGTAACGCC	10
OPA-B06	TGCTCTGCCC	7
OPA-K06	CACCTTTCCC	6
OPA-K17	CCCAGCTGTG	9
OPA-R15	GGACAACGAG	6
OPA-W01	CTCAGTGTCC	8
OPA-X01	CTGGGCACGA	7
OPA-Y01	GTGGCATCTC	5
Total		58

Table 3. Estimates of genetic diversity for *T. indica*.

Population	P	H_S	H
Burkina Faso	65.5	0.325 (0.281)	0.216 (0.199)
Cameroon	77.6	0.429 (0.262)	0.290 (0.186)
Guadeloupe	63.8	0.312 (0.283)	0.207 (0.198)
India	72.4	0.345 (0.268)	0.227 (0.188)
Kenya	75.9	0.401 (0.271)	0.270 (0.193)
Madagascar	60.3	0.326 (0.295)	0.221 (0.208)
Réunion	67.2	0.370 (0.289)	0.251 (0.205)
Senegal	60.3	0.334 (0.299)	0.227 (0.211)
Tanzania	67.2	0.351 (0.287)	0.236 (0.205)
Thailand	39.7	0.219 (0.287)	0.148 (0.200)
	100.0	0.521 (0.180)	0.350 (0.144)

P, percentage of polymorphic loci; H_S, mean Shannon diversity index; H, Nei's diversity index.
Values in parentheses denote standard deviations.

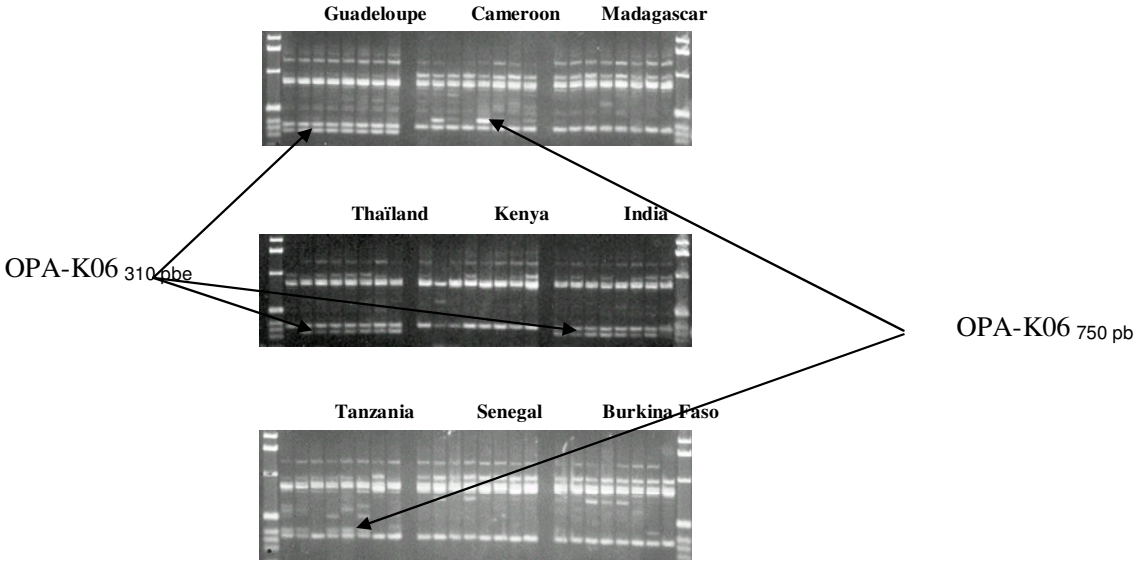

Figure 1. RAPD profiles obtained after amplification of 9 populations of *Tamarindus indica* with OPA-KO6 after separation on a 1.8% agarosse gel. The size marker included was 1 Kb DNA Ladder.

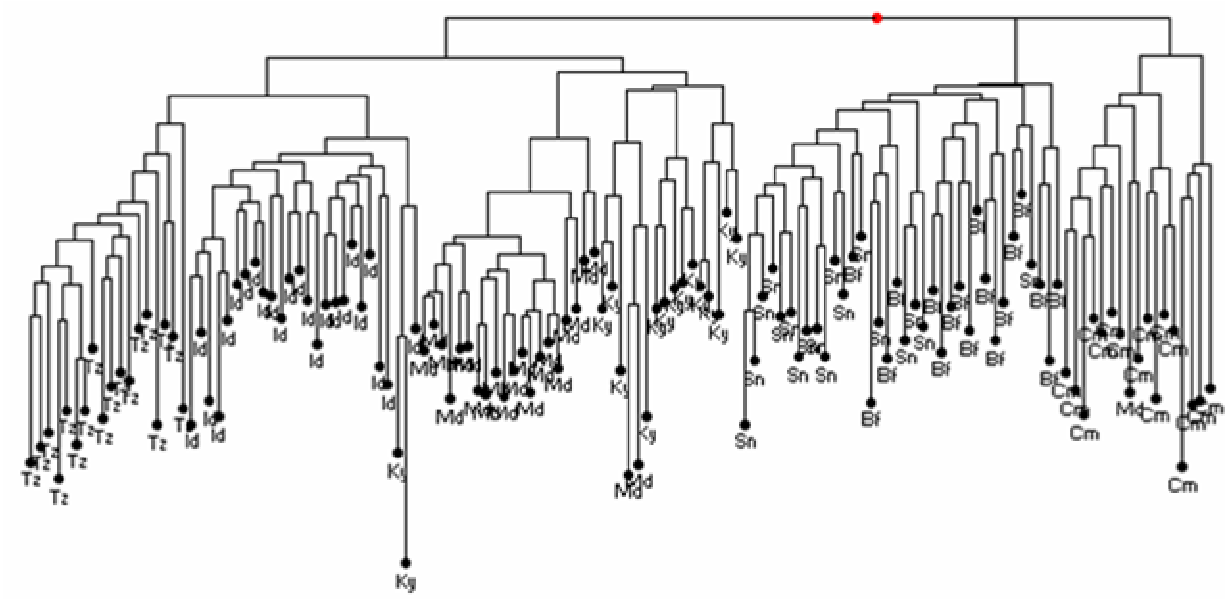

Figure 2. Dendrogram of the populations from native range of *T. indica*, generated by neighbor joining cluster analysis of Sokal and Michener distances. Bf: Burkina Faso; Cm: Cameroon; Id: India; Ky: Kenya; Md: Madagascar; Sn: Senegal; Tz: Tanzania.

The individuals from the potential native range that were grouped into three clusters were analyzed again with the individuals of the population from Thailand, which are planted, and the individuals from Guadeloupe and Réunion, which are from naturalised populations resulting from recent introductions. The dendrogram (Figure 4) shows that individuals from the Réunion are grouped with the western African individuals with a statistically strong bootstrap value (72%); the individuals from Thailand and Guadeloupe form a cluster which is closest to those from Cameroon but with a lower bootstrap value (44%); the individuals from eastern Africa, Madagascar and India are the most different from all the others (bootstrap value of 68%). Thus, a factorial analysis

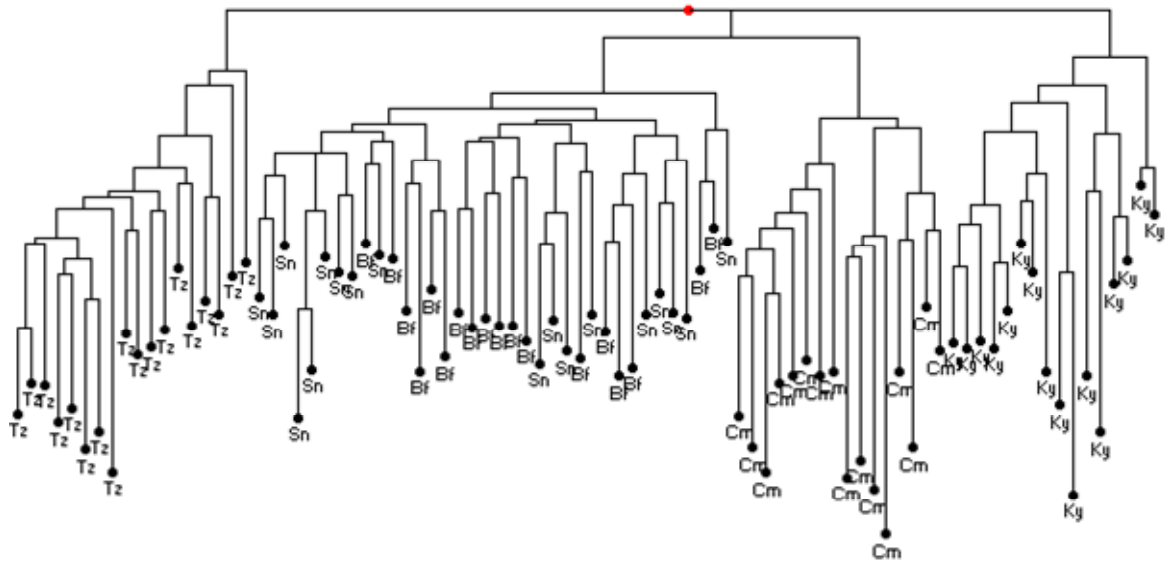

Figure 3. Dendrogram of the African populations generated by neighbour joining cluster analysis of Sokal and Michener distances. Bf: Burkina Faso; Cm: Cameroon; Ky: Kenya; Sn: Senegal; Tz: Tanzania.

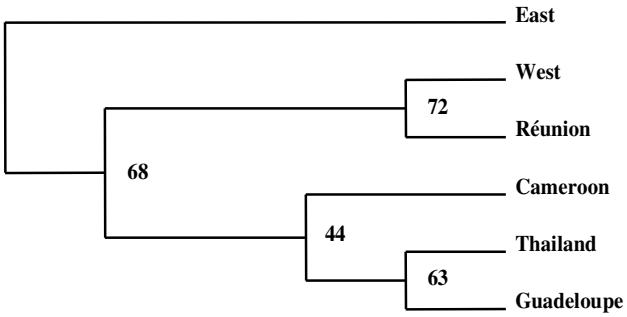

Figure 4. Dendrogram of the various areas considered, constructed using neighbour joining method. Bootstrap values are indicated for each corresponding node (2000 replicates) East: Kenya, Tanzania, Mada-gascar and India; West: Burkina Faso, Senegal.

of correspondence (AFC) (Figure 5) showed the same structuring of populations in addition to predominant markers associated with each group.

DISCUSSION

Presumed origin of *T. indica*

The high intra population variability from the populations of the presumed origins of *T. Indica* do not allow for confirmation of the geographical origin of the species between Africa, Madagascar and India, as the sampling was small in Asia and Madagascar. In fact, Polhill and Raven (1981) who studied the centre of diversity of some Leguminosae tribes measured by the percentage of the total number of genera that are endemic to each region showed that out of the 25 genera of Amhertieae (*Tamarindus* tribe), 23 are endemic to Africa and Madagascar, and only two to Asia and America, respectively. However, our findings reinforce paleontological observations conducted in the tertiary sediments in the south and centre-north of Tanzania respectively, that revealed the presence of the pollen related to five genera of Caesalpinioideae (*Brachystegia*; *Cassia-type didymobotrya*; *Cassia-type italica*; *Isoberlinia* and *Jubernardia-type paniculata*) (Vincens et al., 2003; Herendeen and Jacobs, 2000). According to Polhill and Raven (1981) three of these genera were encountered in the south of central Africa in Guineocongolese forest. However, none of these studies mentioned the *Tamarindus* genus suggesting a very late migration to this zone.

Genetic diversity and origin of newly introduced populations

In general, *T. indica* displays a high genetic diversity (H = 0.38), the value of this species is higher than values obtained with isoenzymes for tropical rain forest species (H = 0.11) (Hamrick and Loveless, 1986) and for Australian *Acacia* species (0.07 to 0.20) (Moran et al., 1989a,b; Coates,1988), or for coniferous species (H = 0.27) (Miton, 1983). In turn, the diversity value of *T. indica* is close to the values reported for *Fadherbia albida* in tropical arid zones (Joly et al., 1992; Harris et al., 1997) and *Prunus africana* (Dawson and Powell,1999). Results obtained in this study are congruent with published studies on other African tree species which indicate a high level of among populations diversity (Lowe et al., 2000),

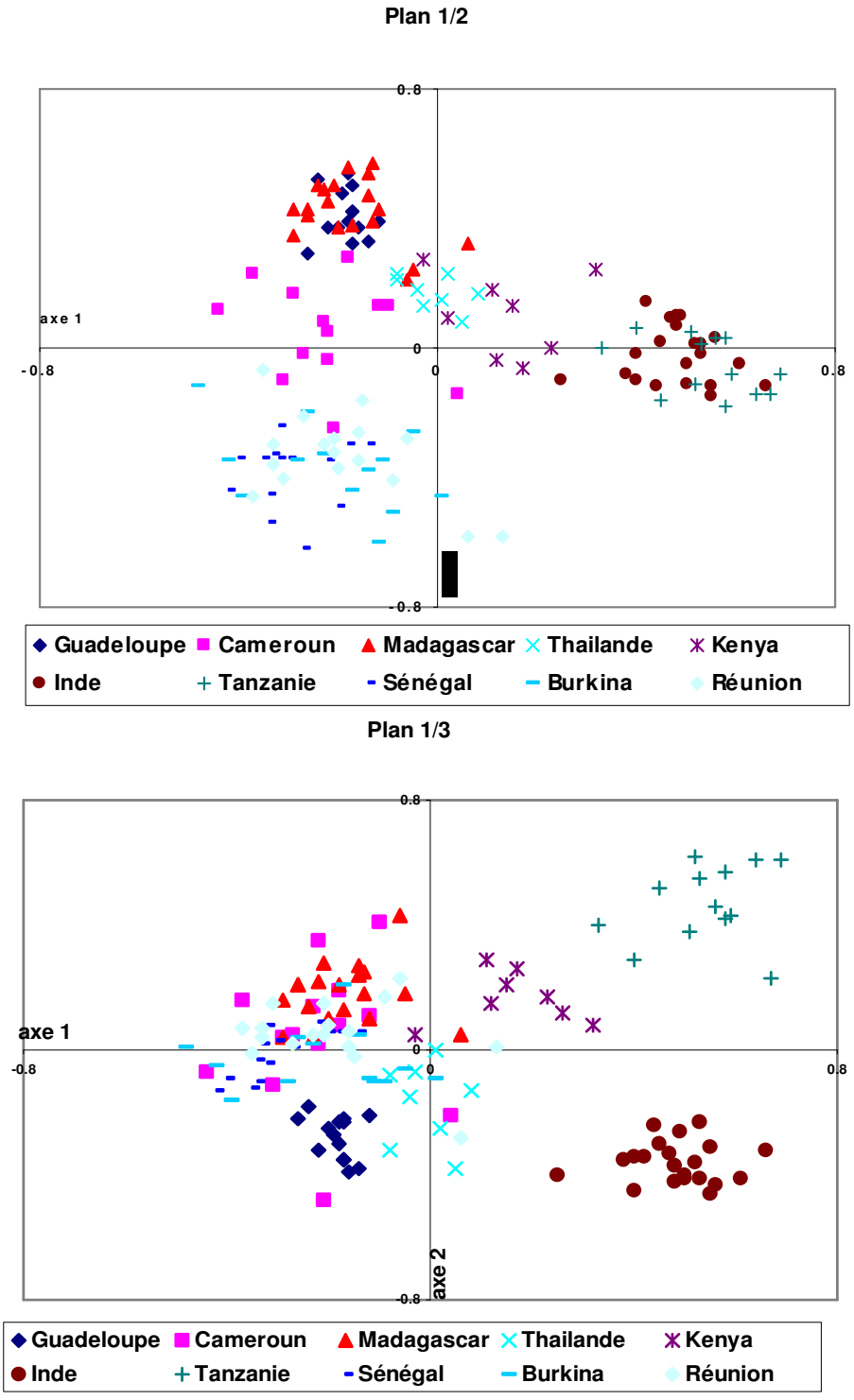

Figure 5. Analyzes Factorial correspondences (AFC) on the individuals (provenances) in plans 1/2 and 1/3.

and a high differentiation between East African and West African populations on *Prunus africana* (Dawson and Powell, 1999), *Faidherbia albida* (Harris et al., 1997) and *Acacia senegal* (Unpublished data Dolmia).

A partial analysis performed on populations coming from the presumed natural distribution of the species (Africa, Madagascar, India) revealed its structure per geographic great region. The partial analysis including only African populations shows a high differentiation between populations from West and East of the continent. Such differentiation has already been found with other species like *F. albida* (Joly et al., 1992; Rendell, 1998), *Ivirginia gabonensis* and *I. wombolu* (Lowe et al., 2000). This differentiation may presumably stem from the role that the Rift valley might have played in stopping gene flow between the two regions of the continent both in terms of seed dispersion and those induced by human exchanges and migration. Moreover, it should be noted that the population from Cameroon displayed the highest genetic diversity value (H = 0.77). This was also found in bush mango (Lowe et al., 2000). The high variability in the Cameroonian population can be explained by two plausible reasons, namely Maroua had been a commercial point between Sub-saharan Africa and India via the Mahgreb using the Sahara road as emphasized by Omer-Cooper et al. (1968), and Cameroon could have been a primary center from which the species migrated toward the other regions of the continent with favorable conditions for its growth.

The two genetically close West African populations presented high intra population diversity that contrast with findings of Chevallier et al. (1994) on Senegal populations of *A. senegal*. However, the contradictory results may be linked to the commercial exchanges in the subregion favoured either by Dioula merchants of nowadays Mali or via the massive displacements of human caravans during transhumance, nomadism and wars. In fact, Omer-Cooper et al. (1968) noted that in the 19th century Fulani (Peulh) conducted many Jihads in the region. The best known example is that of Utsman Dan Fodio in the State of Gobir whose forefathers came from Fouta Toro in actual Senegal. After the fall of the empire, an important part of his fellows went to the northern part of Burkina Faso to create the Liptako. During this second migration, seeds originating from Senegal may have been introduced via Gobir State. Afterward, hybridization of the populations might have happened with the local populations. The second hypothesis is that it might be only one population that never differentiated, because they are geographically isolated. That did not allow the drift effect to impact on populations.

Genetic differentiation of La Réunion from West Africa, and genetic differentiation of Guadeloupe from Thailand populations

Results obtained after analysis of populations from the natural distribution and areas of recent introductions suggest that the population of Réunion Island comes from West Africa. With the discovery of the Island in 1500 by Tristan Da Cunta, the possibilities for Vanilla and sugar cane production led to a need for labour, therefore the first French migrants recruited cheaper labour on the western coasts. These workers may have transported with them seeds of tamarind tree. However, material could have been introduced by Arab merchants who followed the Spanish explorers of the island since medieval times and may have transported seeds to the island. Even though not inhabited, the island was the way to the Indies and may have served as a stop point for boats coming from the western African coasts because the reports relating to the company of Indies (1711) mentioned the presence of this species on the island (Lacouture).http//perso.wanadoo.fr/daniel.lacouture/divers/dossier/nature/culture/nature020/

From this analysis it was also evident that the population of Guadeloupe comes from Thailand. These two populations present also a low genetic diversity compared to the populations from the natural distribution area of the species. This may be due to the fact that the planted trees came from seeds collected on a low number of individuals. The differentiation between the two populations of East Africa (Tanzania and Kenya) is probably due to either natural and/or ethnic barriers (i.e. wars and plundering without occupying the conquered lands) that stopped human movements and indirectly the exchanges of vegetal material.

In conclusion, the intra population variation observed, as well as the low sample number of Asian populations did not allow for clarity on the origin of *T. indica.* However, the observed genetic diversity within the African populations shows that there are no risks of genetic erosion in the short term. Molecular analyses based chloroplastic DNA maternally inherited characteristics may help to understand the mode of dissemination of *T. indica*.

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