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Genetic analysis of mango landraces from Mexico based on molecular markers

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Abstract

Genetic diversity and relationships among 112 mango (*Mangifera indica*) plants native to 16 states of Mexico and four controls [three mango cultivars (Ataulfo, Manila and Tommy Atkins) and one accession of *Mangifera odorata*] were evaluated based on amplified fragment length polymorphism (AFLP) and simple sequence repeat (SSR) molecular markers. Mango germplasm shows broad dispersion through Mexico and genetically similar germplasm from different agroecological regions has previously been found by our group. Both AFLP and SSR analyses indicated high genetic similarity among mango populations that were clustered in two major groups: mangos from Gulf of Mexico coastline and mangos from Pacific Ocean coastline and locations far away from the sea. The highest genetic diversity was found within plants from each state, and significant genetic differentiation ($F_{ST} = 0.1921$, AFLPs and 0.1911, SSRs) was also observed among mango populations based on geographical origin and genetic status (cultivars versus landraces). Heterozygosity values ranged from low (0.38) to moderate (0.68), and no heterozygote deficits were found. The highest genetic variability was found in mango populations from Tabasco, Michoacán and Oaxaca. Data suggested that mangoes are subjected to natural or induced pollination, so segregation as well as genetic recombination plays major roles on genetic diversification of Mexican mangos. AFLP analysis was more robust than SSR for determining the genetic relationships among mango landraces from Mexico.

Keywords: AFLP markers; diversity; germplasm; *Mangifera indica* L. *Mangifera odorata* L.; SSR markers

Introduction

Mangos (*Mangifera indica* L.) have high social and economic impacts on tropical and subtropical regions of Mexico (Ramos, 2003). The main problems of mango production are poor control of tree development, irregular fruit production throughout the tree and susceptibility to freezing, pests and diseases. One or more of those factors frequently reduces fruit yield and quality (Chávez *et al.*, 2001). Breeding of mangos in Mexico has not been constant, and currently mango farmers request bred germplasm from countries such as the USA, as well as open-pollinated trees that are commonly produced through Mexico. The use of open-pollinated trees to replace dead trees in mango orchards has

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increased the genetic diversity of mangoes growing in Mexico. Moreover, open-pollinated trees frequently show better phenotypic attributes compared with landraces or cultivars and must be used as parents for further breeding works. Genetic and phenotypic analyses of native mango germplasm of Mexico could be useful for determining the genetic relationships and diversity among and within landraces generated by open pollination, and for defining the relationships with breed germplasm introduced to the country.

Genetic relationships among breed mango accessions have previously been conducted based on biochemical markers such as isozymes (Degani *et al*., 1990, 1992; Gálvez-López *et al*., 2007) and molecular markers such as random amplified polymorphic DNA (RAPDs; López-Valenzuela *et al*., 1997; Barboza and da Costa, 2004), amplified fragment length polymorphisms (AFLPs; Eiadthong *et al*., 2000; Hernández-Delgado *et al*., 2005) microsatellites [simple sequence repeats (SSRs); Duval *et al*., 2005, 2006; Honsho *et al*., 2005; Schnell *et al*., 2005] and inter-SSRs (Pandit *et al*., 2007). Based on informativeness and robustness, the use of AFLPs and SSRs has been preferred to determine the genetic relationships and dissemination paths in some plant species (Riek *et al*., 2001; Rivera-Ocasio *et al*., 2002). The aims of this work were to analyse, based on AFLP and SSR markers, the genetic relationships among mango landraces of Mexico and to compare them with breed mangos.

Materials and methods

Germplasm

Twenty young leaves from each of 112 mango trees from 16 states of Mexico (seven plants per state) were collected during 2006–2007. Sites of collection included orchards, home gardens, woodlands and land near roads (Table 1). Three mango cultivars (Ataulfo, Manila and Tommy Atkins) from the Germplasm Bank of the Instituto Nacional de Investigaciones Forestales Agropecuarias (INIFAP) located in Cotaxtla, Veracruz, México, as well as one *Mangifera odorata* accession were included as controls.

Genetic analyses

Genomic DNA was isolated by the cetyltrimethylammonium bromide method (Doyle and Doyle, 1987). Germplasm was analysed by using AFLP markers where four AFLP oligonucleotide combinations (*Eco*RI-ACA/*Mse*I-AGT, *Eco*RI-ACA/*Mse*I-ACC, *Eco*RI-ACA/*Mse*I-AGA and *Eco*RI-ACA/*Mse*I-AGG) were used. Combinations were selected after the pre-evaluation of eight oligonucleotide combinations in five selected accessions (Vos *et al*., 1995). Electrophoresis of AFLP products was conducted in one semi-automated sequencer model

Table 1. Sites of collection, common names and collectors of mango landraces throughout 16 states of Mexico

State	Location(s), common name(s)[a] and number of accessions	Collector(s)
Chiapas	Tuxtla Chico (Oro), Escuintla (Amatillo), Tapachula (Coche), Huehuetán (Tapanero), Pijijiapan (Pija, Alcanfor, Piña)	M. Salvador-Figueroa (UNACH)
Campeche	Tixmucuy (Manglona, 2), Chiná ('Tommy Atkins'), Nohacal (Indio, 2; Manila; Manililla)	G. Castañón-Nájera (UJAT)
Tabasco	Teapa (Caramelo), Tumbuluchal (Manila, 2; Pájaro, 2), Villahermosa (Criollo, Manililla)	G. Castañón-Nájera (UJAT)
Nayarit	Ruiz (Manga; Criollo, 2), Santiago Ixcuintla (Criollo, 2; Bola, 2)	J.S. Padilla-Ramírez (INIFAP)
Veracruz	Tuxpan (Criollo, 3), Cd. Cuauhtemoc (Criollo, Petacón, Oro, Durazno)	P.C. Cruz-Romero, D. Gálvez-López (CBG-IPN)
Sinaloa	Guasave (Corriente, Desabrido, Talega, Pera, Naranja, Algodón, Perico)	J. Méndez-Lozano (CIIDIR-IPN)
Guanajuato	Xichú (Criollo, 7)	J.M. González-Prieto (CBG-IPN)
Michoacán	Gabriel Zamora (Criollo, 7)	J.M. González-Prieto (CBG-IPN)
Yucatán	Mérida (Criollo, 7)	R. Zamora-Medina (CINVESTAV-IPN)
Chihuahua	Urique (Manila, 3; Machete, 2; Bola, 2)	H.R. Gill-Langarica (CBG-IPN)
Colima	Tecomán (Criollo, 2), Madrid (Criollo, 2), Jala (Criollo 2), Caleras (Criollo)	M. Orozco-Santos (INIFAP)
Guerrero	Iguala (Criollo 3), Tonalapa (Criollo, 2), Ahuehuetan (Criollo, 2)	J. Rosendo-Escobar (UAGro)
Morelos	Cuautla (Criollo, 2), Cocoyoc (Criollo, 2), Yautepec (Criollo, 2), Anenecuilco (Criollo)	H.E.Flores-Moctezuma(CEPROBI-IPN)
Oaxaca	Chahuites (Chililllo, Jobo, Pico de Loro, Oro, Machete, Pajarito, Manilón)	R. Torres-Cruz
Tamaulipas	Tampico (Mango de Rio; Criollo, 3; Manila; Manililla; Bola)	D. Gálvez-López (CBG-IPN)
San Luis Potosí	Ébano (Criollo, 3; Manzana, Japonés, Tranchete, Bola)	D. Gálvez-López (CBG-IPN)

[a] Number in brackets indicates the number of accessions per local name.

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LICOR IR^2 (Lincoln, NE, EUA) using 6.5% acrylamide gels. Then six SSR loci generated in *M. indica* (Supplementary Table S1, available online only at: http://journals.cambridge.org; Duval *et al.*, 2005) were used to characterize all germplasm. The six SSR loci were pre-selected from ten loci based on amplification patterns and polymorphisms in five selected accessions. Polymerase chain reaction amplification conditions for each SSR locus were described by Duval *et al.* (2005). Amplified fragments were separated by electrophoresis in 6% acrylamide gels and revealed by silver staining (Promega®). Molecular weights of each amplified band were estimated by extrapolation based on the molecular weight of a 25-bp ladder and using a photo-documentation system.

Data analysis

AFLP data

AFLP bands were numbered according to their migration on the gel. One matrix of zeros and ones was constructed and then used to estimate the simple-matching coefficients among accessions (Nei and Li, 1979). One dendrogram based on the neighbour-joining method was constructed using averaged genetic similarity among 16 mango populations (Felsenstein, 2006). Cluster analysis was performed with the software programs Phylip, NJ-Plot and Tree View 1.6.6 (Perrière and Gouy, 1996; Felsenstein, 2006). Average genetic diversity within populations was estimated by calculation of heterozygosity values (H) using Excel Version 2000. The matrix of similarities used for cluster analysis was also used for analysis of molecular variance (AMOVA; Huff *et al.*, 1993; Excoffier *et al.*, 2005) using Arlequin 2.0 (Schneider *et al.*, 1997). The number of permutations for AMOVA's significance tests was 1000 in all cases (Felsenstein, 2004). Bootstrap analysis of AFLP data was performed as described in Felsenstein (2004) and the number of permutations for significance tests was 1000.

SSR data

The molecular weight of each SSR band was used to construct two dendrograms based on neighbour-joining method. One dendrogram including the 16 mango populations was performed as described above. Allele diversity analysis was performed with the software Cervus 2.0 (Marshall *et al.*, 1998), and the number of observed alleles and allele frequencies per locus was calculated, along with the number of analysed accessions and the number of homozygote and heterozygote individuals as well as the values of observed (H_O) and expected (H_E) heterozygosities (Duval *et al.*, 2005). Finally, one AMOVA analysis was performed as been described by AFLP data. Bootstrap analysis of SSR data was performed as described in Felsenstein (2004) and the number of permutations for significance tests was 1000.

Results

AFLP analysis

AFLP analysis produced 308 amplified products, 269 of which were polymorphic (87.3%; data not shown). AMOVA detected significant differences among hierarchies (states of Mexico, populations within states). The highest rate of molecular variance was found in populations within states (80.79%). The fixation index for each hierarchy ($F_{ST} = 0.1921$) indicated high genetic differentiation among and within populations (Table 2). Cluster analysis showed two major groups (Fig. 1). One group included mango populations from Tamaulipas,

Table 2. Analysis of molecular variance of amplified fragment length polymorphism (AFLP) and simple sequence repeat (SSR) data obtained for mango germplasm from Mexico

Source of variation	d.f.	Sum of squares	Variance components	Variation (%)	P
AFLPs					
Among states	15	1482.3	8.8	19.2	<0.01
Populations within state	96	3560.6	37.1	80.8	<0.01
Total	111	5042.9			
SSRs					
Among states	15	131.2	0.5	19.1	<0.01
Populations within state	96	422.4	2.0	80.9	<0.01
Total	111	553.6			

$F_{ST} = 0.1921$ (AFLPs), 0.1911 (SSRs). NS = no significative ($P < 0.05$), ** = significative ($P < 0.01$). d.f., degrees of freedom.

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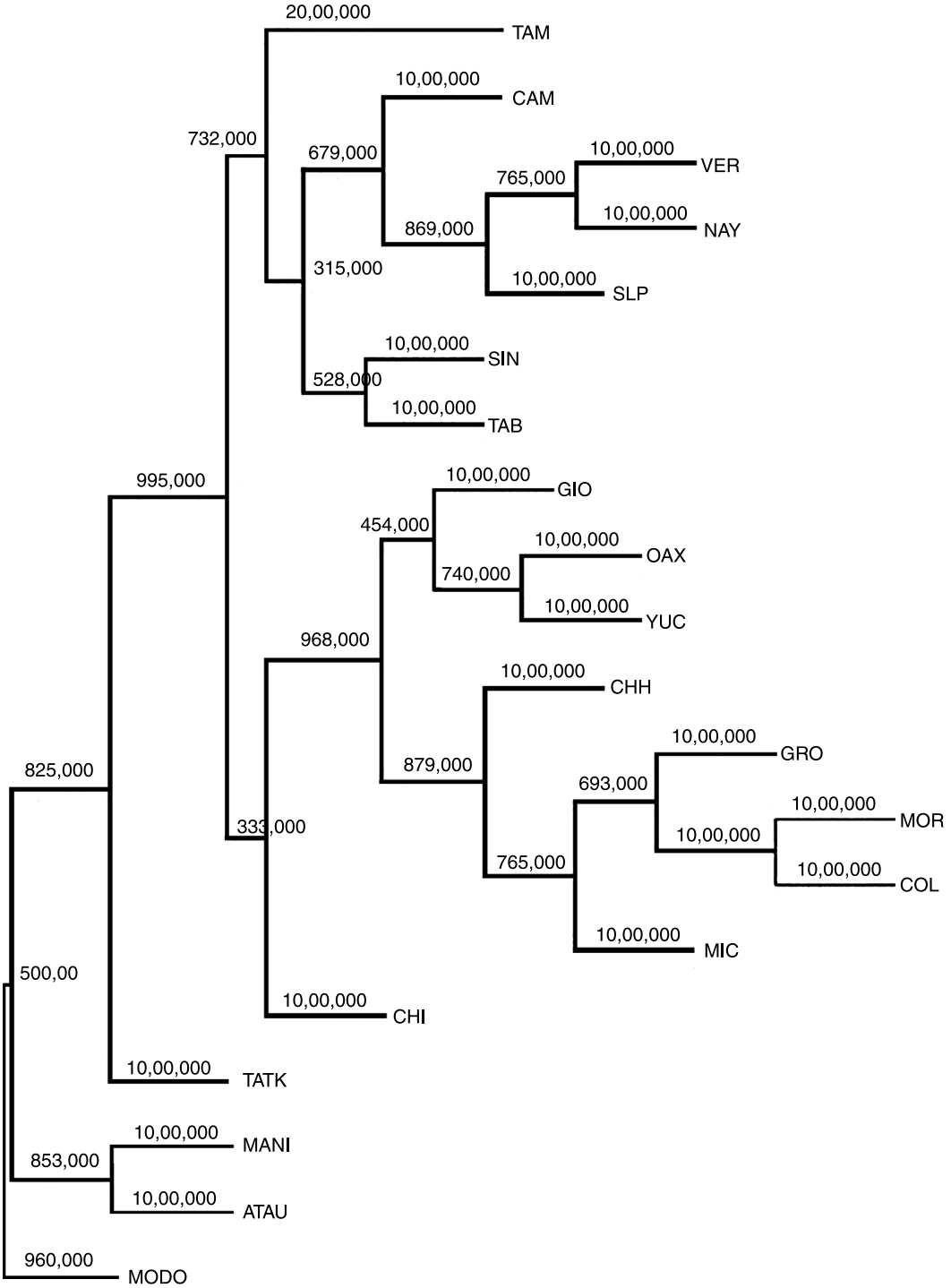

Fig. 1. Bootstrap analysis of 16 mango populations from Mexico based on AFLP markers.

Campeche, Veracruz, Nayarit, San Luis Potosí, Sinaloa and Tabasco, while the other group included mangos from Guanajuato, Oaxaca, Yucatán, Chihuahua, Guerrero, Morelos, Colima, Michoacán and Chiapas. Cultivars Manila, Ataulfo and Tommy Atkins as well as *M. odorata* were separated from Mexican mangos.

SSR analysis

Microsatellite analysis produced 151 alleles (Table 3) and cluster analysis grouped germplasm in two major groups (Fig. 2). One group included populations from Chiapas, Veracruz, San Luis Potosí, Nayarit, Campeche,

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Table 3. Simple sequence repeat data generated from the analysis of mango germplasm from Mexico

Name	*n*	No. of alleles	No. of individuals		Allelic range (bp)		H_O[a]	H_E
			Homozygotic	Heterozygotic	Expected	Observed		
mMCIR008	110	15	92	18	150–170	146–176	0.16	0.87
mMCIR010	110	23	49	61	270–290	250–296	0.56	0.93
mMCIR018	108	19	81	27	216–244	188–244	0.25	0.92
mMCIR022	116	27	12	104	148–190	114–174	0.90	0.94
mMCIR030	113	36	52	61	174–194	154–220	0.54	0.93
mMCIR033	104	31	36	68	154–210	146–210	0.65	0.93
Total/Mean		151	322	339			0.51	0.92

[a] H_O, observed heterozygosity; H_E, expected heterozygosity; bp, base pair.

Tamaulipas, Tabasco and Oaxaca and the other group included that from Chihuahua, Guerrero, Michoacán, Colima, Morelos, Sinaloa, Guanajuato and Yucatán. Cultivars Manila, Ataulfo and Tommy Atkins as well as *M. odorata* were clearly different to Mexican mangos. AMOVA detected significant differences among hierarchies. The highest ratio of molecular variance corresponded to populations within states. The fixation index for hierarchies ($F_{ST} = 0.19\,110$) indicated high genetic differentiation among populations (Table 2). H_E values ranged from 0.546 to 0.841. All amplified SSR loci were polymorphic. Heterozygote individuals per locus ranged from 18 to 104, while homozygote individuals varied from 12 to 92 (Table 3). H_O values were from 0.381 to 0.678 and the highest values were found in mangos from Tabasco, Michoacán and Oaxaca (Table 4). The robustness test indicated that 67 and 40% of AFLP and SSR dendrogram nodes were as consensus dendrogram at least 70% of 1000 permutations, respectively, although both marker systems produced essentially the same mango populations grouping with the exception of populations from Chiapas, Oaxaca and Sinaloa (Figs 1 and 2).

Discussion

Both AFLP and SSR analyses indicated high genetic similarity among mango populations from two clear groups: mangos from Veracruz, Campeche, San Luis Potosí, Nayarit, Tamaulipas and Tabasco (most from the Gulf of Mexico coastline) and mangos from Chihuahua, Guerrero, Michoacán, Colima, Morelos, Guanajuato and Yucatán (most from Pacific Ocean coastline and locations far away from the sea). Both marker systems produced similar mango clustering with the exception of those from Chiapas, Oaxaca and Sinaloa. Polymorphism percentages are higher than those reported by López-Valenzuela *et al.* (1997), Eiadthong *et al.* (2000) and Hernández-Delgado *et al.* (2005) due to the fact that they used mango germplasm from banks with high percentages of cultivars and high ratios of parentage. Significant differences among populations by state indicated a high genetic variation in Mexican mango germplasm and relative reproductive isolation, with differentiated patterns of recombination due to the genetic recombination and segregation in each agroecological environment; in addition, we found relative differentiation among original mango populations introduced to Mexico from Asia. Former genetic structure delimits genetic differences that could be increased by the reproductive isolation. Mono- and poly-embryonic mangos were introduced to Mexico, although it remains unclear which types were introduced at each original point of introduction. After that, mangos were naturally and artificially dispersed through Mexico by seeds (Eiadthong *et al.*, 2000). High genetic differentiation values indicated the probable fixation of new alleles in specific populations as well as recombination and segregation and selection of the best genes by open pollination of genetically different mangos (Rivera-Ocasio *et al.*, 2002). Mango cultivars were different from all native mangos due to genetic recombination, segregation and selection of better genotypes in the former introduced mangos, which produced genetically different mango lineages compared with mango cultivars (Hernández-Delgado *et al.*, 2005). However, data indicated that former mango introductions could be highly heterozygote and/or high levels of natural/induced recombination may have happened (Honsho *et al.*, 2005). Further work should take into account germplasm provenances in order to estimate genetic variability that can be detected in the analysed material (Rivera-Ocasio *et al.*, 2002). An extensive phylogenetic study using mtDNA might be able to reveal the precise parentage and phylogeny among Mexican mango populations (Moritz, 1994).

The allelic range found in our SSR analysis was broader than that reported by Duval *et al.* (2005), who worked with breed germplasm and provided evidence that high recombination and/or migration and gene flux has occurred in Mexican mangos. Our data suggest that

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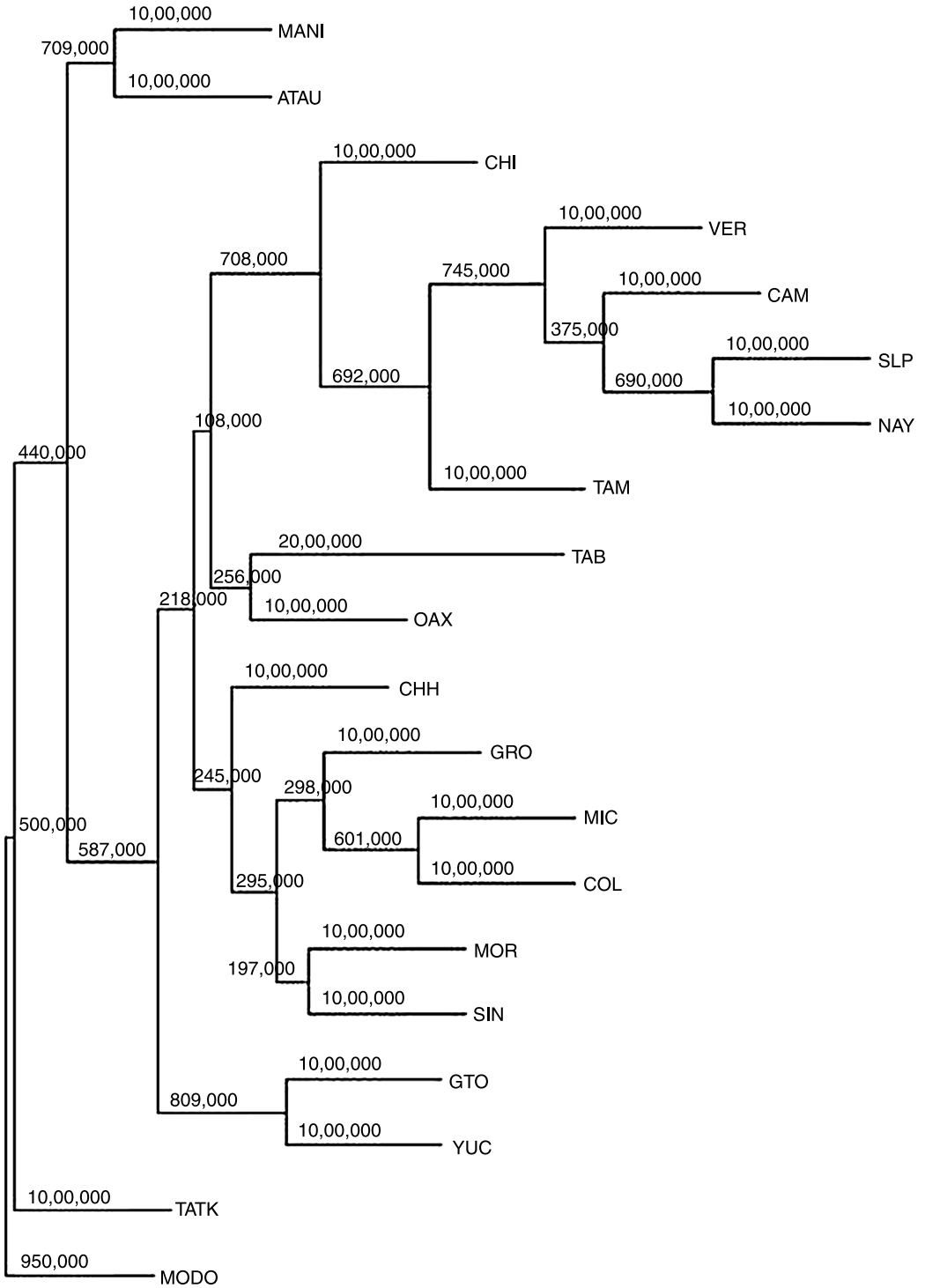

Fig. 2. Bootstrap analysis of 16 mango populations from Mexico based on SSR markers.

locus mMiCIR022 could be used for mango germplasm analysis due the high polymorphic content that can be detected in Mexican mangos. Despite a heterozygote range that ranged from low to moderate, no heterozygote deficits were found and mango germplasm showed significant genetic differences due to random crossing among landraces (Schnell *et al.*, 2005). Honsho *et al.* (2005) reported heterozygote ranges from 0 to 0.83 after analysing mangos from Thailand. The SSR values were lower than that reported in this research, mainly due to the fact that the germplasm analysed by these authors was obtained from a Germplasm Bank and was

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Table 4. Heterozygosity in 16 mango populations from Mexico obtained based on simple sequence repeat marker data

	Averaged heterozygosity	
State	H_O[a]	H_E
Chiapas	0.52	0.84
Campeche	0.50	0.73
Nayarit	0.43	0.65
San Luis Potosí	0.38	0.75
Veracruz	0.40	0.80
Tamaulipas	0.50	0.77
Sinaloa	0.57	0.78
Tabasco	0.68	0.82
Guanajuato	0.39	0.82
Yucatán	0.50	0.78
Oaxaca	0.61	0.80
Chihuahua	0.55	0.80
Colima	0.39	0.57
Michoacán	0.64	0.63
Guerrero	0.57	0.64
Morelos	0.43	0.72
Mean	0.50	0.74

[a] H_O, observed heterozygosity; H_E, expected heterozygosity.

genetically bred, with high levels of parentage. Schnell *et al.* (2005) reported heterozygosity values of 0.241–0.712 after analysing mango cultivars from Florida, USA, using SSRs. Germplasm analysed in this work was also highly related and was subjected to constant selection and clonal propagation, which may have reduced genetic diversity. Duval *et al.* (2005) found heterozygosity values from 0.059 to 0.857 in mangos from one Germplasm Bank located in Guadalupe, although they did not mention the origin of the germplasm. Our highest heterozygosity values were detected in mango populations from Tabasco, Michoacán and Oaxaca, which suggests high levels of natural or induced recombination.

AFLP markers have been assessed and confirmed as a robust strategy to establish differentiation degrees, identification of genotypes and precise genetic relationships in a broad diversity of plant species (Mueller and Wolfenbarger, 1999; Eiadthong *et al.*, 2000; Rivera-Ocasio *et al.*, 2002). In addition, SSRs are very sensitive for genetic variability characterization, genotype and individual identification, and parentage definition among single individuals, as compared with dominant marker strategies such as AFLPs or RAPDs. One advantage of SSRs over dominant markers is that co-dominant markers can determine the population genetic structure and identify shared alleles among individuals (Sun *et al.*, 1999). Bootstrap analyses of both AFLP and SSR data indicated that AFLPs are more robust than microsatellites for Mexican mango germplasm genotyping. For the establishment of genetic relationships and estimation of genetic diversity in mango germplasm, AFLP markers supply statistically reliable and robust information, although SSRs are a reliable marker strategy to determine parentages and ancestors among mango genotypes (Duval *et al.*, 2005; Honsho *et al.*, 2005; Schnell *et al.*, 2005).

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