

Global Genetic Diversity and Population Structure of Mango (*Mangifera indica* L.) Germplasm Conserved in Oman Revealed Through SSR Markers

Abdullah Al-Jabri

aljabriabdullah@hotmail.com

Ministry of Agriculture, Fisheries and Water Resources

AL-Ghaliya AL-Mamari

Ministry of Agriculture, Fisheries and Water Resources

Ali Al-Adawi

Ministry of Agriculture, Fisheries and Water Resources

Muhammed Al-Jabri

Ministry of Agriculture, Fisheries and Water Resources

Wafa Al-Shibli

Ministry of Agriculture, Fisheries and Water Resources

Muna Al-Jabri

Ministry of Agriculture, Fisheries and Water Resources

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Abstract

Mangifera indica L. (mango) is a major tropical fruit tree valued for its nutritional, economic, and cultural importance. Understanding the genetic diversity within mango germplasm is essential for conservation and for selecting parents in breeding programs. This study assessed the genetic variation of 126 mango accessions (378 samples) maintained in the National Mango GenBank in Oman, originating from 15 geographical regions across the Middle East, Africa, Asia, Australia, and the Americas. A total of 55 polymorphic SSR loci generated 706 alleles, averaging 12.8 alleles per locus, with allele number ranging from 4 (MiSHRS-23, MGDSSR17) to 25 (MiSHRS-18). Polymorphic information content (PIC) values ranged from 0.184 (SSR22) to 0.903 (LMMA01), indicating high marker informativeness. Expected and observed heterozygosity ranged between 0.024–0.496 and 0.048–0.992, respectively. Fixation indices (Fis, Fit, Fst) averaged – 0.978, 0.430, and 0.714, reflecting excess heterozygosity within accessions and strong differentiation among populations. Molecular variance partitioned approximately 87% of diversity among populations and 13% within populations. Cluster, PCoA, and STRUCTURE analyses separated accessions into two major genetic groups, with Oman forming a distinct cluster alongside a small number of foreign cultivars. This study demonstrates extensive genetic diversity in Oman's mango germplasm and highlights SSR markers as an effective tool for distinguishing genotypes. The findings provide a critical foundation for cultivar preservation, parent selection, and future genome-wide association and marker-assisted breeding in mango.

Introduction

Mango (*Mangifera indica* L.) is one of the world's most important perennial fruit crops, widely cultivated across tropical and subtropical regions. Belonging to the family Anacardiaceae, its primary centre of origin is believed to lie within Southeast Asia, particularly the Malay Archipelago (Viruel et al., 2005; Mukherjee and Litz, 2009; Pérez et al., 2019). The fruit is globally valued for its flavour, nutritional quality, and commercial significance. In Oman, mango is the fourth most cultivated fruit crop after date palm, citrus and banana, with historical records indicating its first introduction between 1568–1575 AD in Wilayat Ibri, Al Dhahirah Governorate (Al Busaidi, 2008; Al Salmi, 1997). Current estimates suggest that Oman hosts more than half a million mango trees, producing approximately 15,673 tonnes in 2016 with an estimated value exceeding USD 9 million (MAFWR, 2012).

Despite its long cultivation history, mango production in Oman has been negatively affected by the emergence of wilt disease caused by *Ceratocystis manginecans*, frequently vectored by the bark beetle *Hypocryphalus mangiferae* (Van Wyk et al., 2007; Al Adawi et al., 2006; Plotez and Freeman, 2009). The epidemic led to widespread mortality of mature indigenous trees, resulting in the loss of important genetic lines. Local cultivars, commonly seed-derived and genetically diverse due to natural outcrossing, have been shown to be highly susceptible to wilt in both Oman and Pakistan (Panhwar et al., 2008; Al Adawi et al., 2006). Many existing landraces are characterised by large tree size, irregular bearing, fibrous pulp and acidic flavour profiles (MAF, 1990), reinforcing the need for improved disease-tolerant and high-quality genotypes.

Understanding the genetic variation preserved in germplasm collections is fundamental for breeding, conservation, and long-term resource management. Population diversity is shaped by mutation, gene flow, breeding system, selection, drift and demographic history (Van Zonneveld et al., 2014; Moran, 2002; Verde et al., 2013). Molecular markers, particularly simple sequence repeats (SSRs), have become powerful tools for such studies due to their high polymorphism, co-dominance, repeatability, and genome-wide distribution (Joop Ouborg et al., 2009; Edwards et al., 2012). SSRs have previously been employed for mango diversity assessment in India, Australia, Mexico, the Caribbean, and Oman (Duval et al., 2006; Schnell et al., 2006; Dillon et al., 2013; Al-Washahi *et al.*, 2017).

However, existing studies on Omani mango germplasm have been limited to locally collected material and have not integrated a broad comparative dataset representing global origins. Given Oman's history as a centre of agricultural exchange and maritime trade, imported germplasm may have significantly contributed to the modern varietal pool (Hammer et al., 2009). A comprehensive molecular evaluation integrating foreign genetic resources is therefore essential.

This study aimed to characterise the genetic diversity of mango germplasm maintained in Oman using informative SSR markers. Specifically, we sought to:

1. Evaluate SSR marker suitability for detecting polymorphism across diverse mango accessions
2. Assess genetic relationships among local and internationally derived cultivars using allelic diversity, heterozygosity and F-statistics.
3. Determine population structure, clustering patterns, and possible introgression between Omani and non-Omani genotypes.

The outcomes provide a molecular foundation for cultivar conservation, genetic improvement and selection of elite parental lines for future breeding initiatives in Oman.

Materials and Methods

Plant Material

A total of 126 mango accessions were obtained from the National Mango GenBank at the Sohar Agricultural Research Station in Oman (N 24.3196277, E 56.7155988). Each accession was represented by three independent biological replicates, maintained as separate trees to ensure clonal identity and long-term phenotypic consistency. Young, healthy leaf tissue was collected for DNA extraction (Fig. 1). The accessions represented cultivars from 15 geographical regions: Oman (26), Australia (24), India (24), Brazil (17), Thailand (11), Indonesia (3), Indochina (3), Malaysia (3), USA (5), Vietnam (5), Israel (1), Philippines (1), Sri Lanka (1), Tahiti (1), and Kenya (1). Of the total accessions, 58 were monoembryonic and 68 polyembryonic. A full list of accessions, origin and seed type is provided in Supplementary Table 1.

DNA Extraction and Quantification

Genomic DNA was extracted from fresh leaf tissue using the DNeasy Plant Mini Kit (Qiagen, Germany) following the manufacturer's protocol with minor optimization. Briefly, 100 mg of leaf powder was incubated in 400 µl of AP1 buffer and 4 µl RNase A at 65°C for 10 min. After addition of 130 µl P3 buffer and ice incubation for 5 min, samples were centrifuged and the supernatant passed through QIAshredder columns. DNA binding, washing, and elution were performed using DNeasy spin columns, with final elution in 50 µl AE buffer. DNA purity was visualized on 1% agarose gel stained with ethidium bromide. DNA concentration was measured using NanoDrop 8000 (Thermo Scientific, USA), and samples were diluted to 30 ng/µl for downstream use.

SSR Amplification and Genotyping

A total of 106 mango specific SSR primers developed by Duval et al. (2005); Viruel et al. (2005); Honsho et al. (2005); Schnell et al. (2005); Begum et al. (2013); and Surapaneni et al. (2013) were initially tested for amplification. Of these, 55 loci (51.9%) showing clear amplification and polymorphism were selected for final genotyping. Twenty-eight loci were monomorphic and 23 showed no amplification (Supplementary Table 2).

PCR amplification was performed in 25 µl reactions containing: 10× PCR buffer with MgCl₂ (Thermo Scientific), 10 mM dNTPs, 10 µM forward and reverse primers, 0.5 U Taq DNA polymerase and 30 ng genomic DNA. Forward primers were fluorescently WellRed-labelled (5'-CACGACGTTGTAAAACGAC-3'). Thermal cycling conditions consisted of: 95°C for 4 min; 35 cycles of 95°C for 30 s, 50–60°C for 1 min (primer-dependent), 72°C for 1 min; and final extension at 72°C for 7 min. PCR products were separated on 2% agarose, and final fragment analysis was conducted on CEQ8000 DNA analyzer (Beckman Coulter, USA). Allele peaks were scored using Beckman Coulter Software v8.0.52. Each sample was run 2–3 times for scoring accuracy and allele size stability.

Genetic Diversity and Statistical Analysis

Allele scoring, fragment sizing, and internal size calibration were performed with the CEQ8000 platform. PowerMarker v3.25 (Liu and Muse, 2005) was used to calculate Polymorphic Information Content (PIC). GenAlEx v6.5 (Peakall and Smouse, 2012) was used for Nei's genetic distance (Nei, 1978), percentage of polymorphic loci, and Analysis of Molecular Variance (AMOVA), Total alleles, Effective alleles (Ne), Observed (Hobs) and expected heterozygosity (Hexp), Wright's fixation indices (Fis, Fst, Fit). Population relationships were visualized using Principal Coordinate Analysis (PCoA) based on Nei's distance matrix.

Phylogenetic clustering was performed using DARwin v6.0 (Perrier and Jacquemoud-Collet, 2006) with UPGMA/Neighbor-Joining unrooted trees. Bayesian population structure was inferred using STRUCTURE v2.3.4 (Pritchard et al., 2000) with an admixture model, burn-in of 100,000 and 1,000,000 MCMC

iterations for $K = 1-10$, repeated 10 times. Optimal K was determined by using ΔK method (Evanno et al., 2005) via STRUCTURE Harvester (Earl and vonHoldt, 2012).

Results

SSR Marker Screening and Polymorphism

Out of 106 SSR markers screened across 126 mango accessions, 55 loci (51.9%) amplified successfully and exhibited polymorphism. Twenty-eight loci (26.4%) were monomorphic and excluded, while 23 loci (21.7%) did not amplify reliably (Supplementary Table 2). The selected 55 markers generated a total of 706 alleles, averaging 12.8 alleles per locus, demonstrating high genetic informativeness.

Allele number ranged from 4 at MiSHRS-23 and MGDSSR17 to 25 at MiSHRS-18. PIC values varied widely (0.184–0.903) with mean 0.700, indicating that most loci were highly polymorphic. Six loci exhibited $PIC < 0.5$, while the remaining 49 loci were moderately to highly informative (Table 1).

Allele size ranged from 101 bp (MiSHRS-18) to 345 bp (SSR24). Representative electropherograms show clear peak distinction in heterozygous (two-peak) and homozygous (single-peak) genotypes (Figure 2B-C).

Table 1. Allelic size range, Number of alleles, expected heterozygosity (H_{exp}), observed heterozygosity (H_{obs}), Effective number of alleles (N_e) and the PIC for 55 microsatellite loci calculated with the mean estimate of different parameters for the Mango accessions.

Locus Name	Allelic size range (bp)	Number of alleles	H_{exp}	H_{obs}	N_e	PIC
LMMA01	202-230	17	0.226	0.452	1.452	0.903
LMMA08	274-291	15	0.266	0.532	1.532	0.819
LMMA10	170-200	17	0.242	0.484	1.484	0.824
LMMA11	250-273	14	0.226	0.452	1.452	0.841
LMMA12	215-228	11	0.278	0.556	1.556	0.768
LMMA15	224-242	16	0.238	0.476	1.476	0.832
LMMA02	295-320	10	0.063	0.127	1.127	0.523
LMMA03	121-174	15	0.425	0.849	1.849	0.813
LMMA04	242-269	12	0.266	0.532	1.532	0.672
LMMA07	220-243	14	0.274	0.548	1.548	0.781
LMMA09	187-227	21	0.270	0.540	1.540	0.855
LMMA16	251-262	10	0.226	0.452	1.452	0.726
MIAC-05	135-177	19	0.270	0.540	1.540	0.894
mMiCIR010	295-316	15	0.163	0.325	1.325	0.698
MiSHRS-18	101-133	25	0.417	0.833	1.833	0.901
MiSHRS-32	221-239	9	0.198	0.397	1.397	0.415
MiSHRS-37	130-153	6	0.101	0.148	1.202	0.188
MiSHRS-39	222-390	12	0.258	0.516	1.516	0.749
MiSHRS-01	211-238	11	0.127	0.254	1.254	0.798
MiSHRS-04	142-151	7	0.032	0.063	1.063	0.609
MiSHRS-23	220-225	4	0.052	0.103	1.052	0.561
MiSHRS-29	192-203	9	0.119	0.238	1.238	0.590
MiSHRS-33	253-271	12	0.099	0.198	1.198	0.576
MiSHRS-36	193-211	6	0.095	0.190	1.190	0.668
MiSHRS-48	216-317	19	0.079	0.159	1.159	0.859
SSR-18	103-134	17	0.274	0.548	1.548	0.707
SSR-20	112-133	7	0.286	0.571	1.571	0.537
SSR-28	256-286	6	0.417	0.833	1.833	0.746

SSR-41	149-260	22	0.151	0.302	1.302	0.849
SSR-82	228-282	19	0.167	0.333	1.333	0.819
SSR-85	173-289	20	0.183	0.365	1.365	0.858
SSR-90	204-222	8	0.238	0.476	1.476	0.668
SSR-91	256-268	7	0.079	0.159	1.159	0.451
MngSSR-14	176-193	15	0.143	0.286	1.286	0.655
SSR16	155-188	21	0.119	0.238	1.238	0.835
SSR17	201-218	11	0.131	0.262	1.262	0.580
SSR22	212-218	6	0.024	0.048	1.048	0.184
SSR24	331-345	9	0.175	0.349	1.349	0.669
SSR26	184-206	14	0.226	0.452	1.452	0.777
SSR29	172-188	12	0.202	0.405	1.405	0.689
SSR34	167-187	11	0.246	0.492	1.492	0.621
SSR36	223-254	15	0.143	0.286	1.286	0.843
SSR37	167-288	9	0.194	0.389	1.389	0.808
SSR39	165-203	19	0.274	0.548	1.548	0.880
SSR49	259-284	13	0.250	0.500	1.500	0.735
SSR83	211-241	20	0.345	0.690	1.690	0.887
SSR84	231-268	16	0.226	0.452	1.452	0.843
MNGSSR18	160-165	6	0.071	0.143	1.143	0.697
MGDSSR2	220-281	8	0.198	0.397	1.397	0.564
MGDSSR5	212-247	9	0.167	0.333	1.333	0.681
MGDSSR6	207-246	10	0.103	0.206	1.206	0.705
MGDSSR11	212-228	11	0.234	0.468	1.468	0.784
MGDSSR17	188-202	4	0.496	0.992	1.992	0.404
MGDSSR22	117-201	23	0.375	0.503	1.877	0.840
MGDSSR24	160-179	12	0.083	0.167	1.167	0.434
Mean		12.8	0.204	0.403	1.409	0.700

Figure 2. (A) The percentage of polymorphic loci in mango cultivars was determined using GenAlex. (B) Heterozygous allele showing 2 peaks for Dura accession using MGDSSR5. Scoring was performed using Beckman coulter software. The y-axis represents the maximum height of the peak, while the x-axis represents the size of the peak in terms of base pairs. (C) Homozygous allele shows only 1 peak for Alphonso accession using MiSHRS-33. Scoring was performed using Beckman coulter software. The y-axis represents the maximum height of the peak, while the x-axis represents the size of the peak in terms of base pairs.

Genetic diversity

Genetic differences in 126 mango accessions were analysed using 55 microsatellite primer pairs, resulting in the detection of 706 alleles. The mean number of alleles per locus was 12.8. The locus MiSHRS-23 and MGDSSR17 had 4 alleles, while the locus MiSHRS-18 had 25 alleles (Table 1). The homozygous alleles were characterized by a single peak, while the heterozygous alleles displayed two peaks (refer to Figure 2 B&C). The allele size for these loci ranged from 101 bp for the locus MiSHRS-18 to 345 bp for the locus SSR24, as showed in Table 1. The number of effective alleles (N_e) varied, with a range of 1.048 for the SSR22 locus to 1.992 for the MGDSSR17 locus, resulting in an average of 1.409 per locus. Calculations for PIC values were based on the frequency and number of alleles at specific loci. The current study found that the average PIC value for the 55 loci evaluated varied from 0.184 for SSR22 to 0.903 for LMMA01, with an overall average of 0.700 across all markers. This indicates that the mango germplasm analysed had a significant degree of polymorphism for most of the loci studied (Table 3).

Figure 2. (A) The percentage of polymorphic loci in mango cultivars was determined using GenAlex. (B) Heterozygous allele showing 2 peaks for Dura accession using MGDSSR5. Scoring was performed using Beckman coulter software. The y-axis represents the maximum height of the peak, while the x-axis represents the size of the peak in terms of base pairs. (C) Homozygous allele shows only 1 peak for Alphonso accession using MiSHRS-33. Scoring was performed using Beckman coulter software. The y-axis represents the maximum height of the peak, while the x-axis represents the size of the peak in terms of base pairs.

Heterozygosity and fixation index

Table 1 shows the presence of moderate levels of observed and expected heterozygosity. The average H_{exp} values of the mango accessions ranged from 0.024 (SSR22) to 0.496 (MGDSSR17), with an average of 0.204 across all loci. The H_{obs} values for all markers varied from 0.048 (SSR22) to 0.992 (MGDSSR17), with an average of 0.403. The cultivars exhibited a range of polymorphic loci percentages, with values ranging from 20% to 67.27%, and an average of 40.59% (Figure 2A).

The F_{is} (fixation index or inbreeding coefficient of individuals relative to subpopulations (Wright, 1965) representing the heterozygous deficiency related to the existence of a reproduction within a subpopulation) values for all markers varied between -1.000 (most loci) and -0.341 (MGDSSR22) per primer with an average of -0.978, reflecting heterozygosity excess and low inbreeding. As for the F_{it} , the

values were ranged from -0.911 (MGDSSR17) to 0.902 (MiSHRS-04) with an average of 0.430, indicating moderate differentiation when considering entire population. The F_{st} values, which represent the fixation index of subpopulations compared to the whole population (Wright, 1969), ranged from 0.045 (MGDSSR17) to 0.951 (MiSHRS-04), with an average of 0.714, demonstrating high genetic divergence among geographic origins (Table 2). These values collectively indicate low inbreeding within accessions, but substantial divergence among populations.

Table 1. Allelic size range, Number of alleles, expected heterozygosity (H_{exp}), observed heterozygosity (H_{obs}), Effective number of alleles (N_e) and the PIC for 55 microsatellite loci calculated with the mean estimate of different parameters for the Mango accessions.

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LMMA10	170-200	17	0.242	0.484	1.484	0.824
LMMA11	250-273	14	0.226	0.452	1.452	0.841
LMMA12	215-228	11	0.278	0.556	1.556	0.768
LMMA15	224-242	16	0.238	0.476	1.476	0.832
LMMA02	295-320	10	0.063	0.127	1.127	0.523
LMMA03	121-174	15	0.425	0.849	1.849	0.813
LMMA04	242-269	12	0.266	0.532	1.532	0.672
LMMA07	220-243	14	0.274	0.548	1.548	0.781
LMMA09	187-227	21	0.270	0.540	1.540	0.855
LMMA16	251-262	10	0.226	0.452	1.452	0.726
MIAC-05	135-177	19	0.270	0.540	1.540	0.894
mMiCIR010	295-316	15	0.163	0.325	1.325	0.698
MiSHRS-18	101-133	25	0.417	0.833	1.833	0.901
MiSHRS-32	221-239	9	0.198	0.397	1.397	0.415
MiSHRS-37	130-153	6	0.101	0.148	1.202	0.188
MiSHRS-39	222-390	12	0.258	0.516	1.516	0.749
MiSHRS-01	211-238	11	0.127	0.254	1.254	0.798
MiSHRS-04	142-151	7	0.032	0.063	1.063	0.609
MiSHRS-23	220-225	4	0.052	0.103	1.052	0.561
MiSHRS-29	192-203	9	0.119	0.238	1.238	0.590
MiSHRS-33	253-271	12	0.099	0.198	1.198	0.576
MiSHRS-36	193-211	6	0.095	0.190	1.190	0.668
MiSHRS-48	216-317	19	0.079	0.159	1.159	0.859
SSR-18	103-134	17	0.274	0.548	1.548	0.707
SSR-20	112-133	7	0.286	0.571	1.571	0.537
SSR-28	256-286	6	0.417	0.833	1.833	0.746

SSR-41	149-260	22	0.151	0.302	1.302	0.849
SSR-82	228-282	19	0.167	0.333	1.333	0.819
SSR-85	173-289	20	0.183	0.365	1.365	0.858
SSR-90	204-222	8	0.238	0.476	1.476	0.668
SSR-91	256-268	7	0.079	0.159	1.159	0.451
MngSSR-14	176-193	15	0.143	0.286	1.286	0.655
SSR16	155-188	21	0.119	0.238	1.238	0.835
SSR17	201-218	11	0.131	0.262	1.262	0.580
SSR22	212-218	6	0.024	0.048	1.048	0.184
SSR24	331-345	9	0.175	0.349	1.349	0.669
SSR26	184-206	14	0.226	0.452	1.452	0.777
SSR29	172-188	12	0.202	0.405	1.405	0.689
SSR34	167-187	11	0.246	0.492	1.492	0.621
SSR36	223-254	15	0.143	0.286	1.286	0.843
SSR37	167-288	9	0.194	0.389	1.389	0.808
SSR39	165-203	19	0.274	0.548	1.548	0.880
SSR49	259-284	13	0.250	0.500	1.500	0.735
SSR83	211-241	20	0.345	0.690	1.690	0.887
SSR84	231-268	16	0.226	0.452	1.452	0.843
MNGSSR18	160-165	6	0.071	0.143	1.143	0.697
MGDSSR2	220-281	8	0.198	0.397	1.397	0.564
MGDSSR5	212-247	9	0.167	0.333	1.333	0.681
MGDSSR6	207-246	10	0.103	0.206	1.206	0.705
MGDSSR11	212-228	11	0.234	0.468	1.468	0.784
MGDSSR17	188-202	4	0.496	0.992	1.992	0.404
MGDSSR22	117-201	23	0.375	0.503	1.877	0.840
MGDSSR24	160-179	12	0.083	0.167	1.167	0.434
Mean		12.8	0.204	0.403	1.409	0.700

Table 2. *F*-statistics (F_{is} , F_{it} and F_{st}) values among all population for each locus with the estimated mean for each parameter.

Locus Name	F_{is}	F_{it}	F_{st}
LMMA01	-1.000	0.502	0.751
LMMA08	-1.000	0.366	0.683
LMMA10	-1.000	0.424	0.712
LMMA11	-1.000	0.472	0.736
LMMA12	-1.000	0.303	0.652
LMMA15	-1.000	0.439	0.720
LMMA02	-1.000	0.771	0.885
LMMA03	-1.000	-0.021	0.489
LMMA04	-1.000	0.260	0.630
LMMA07	-1.000	0.314	0.657
LMMA09	-1.000	0.378	0.689
LMMA16	-1.000	0.398	0.699
MIAC-05	-1.000	0.402	0.701
mMiCIR010	-1.000	0.547	0.774
MiSHRS-18	-1.000	0.083	0.541
MiSHRS-32	-1.000	0.096	0.548
MiSHRS-37	-0.461	0.242	0.481
MiSHRS-39	-1.000	0.337	0.668
MiSHRS-01	-1.000	0.690	0.845
MiSHRS-04	-1.000	0.902	0.951
MiSHRS-23	-1.000	0.324	0.865
MiSHRS-29	-1.000	0.616	0.808
MiSHRS-33	-1.000	0.682	0.841
MiSHRS-36	-1.000	0.733	0.867
MiSHRS-48	-1.000	0.818	0.909
SSR-18	-1.000	0.266	0.633
SSR-20	-1.000	0.014	0.507
SSR-28	-1.000	-0.071	0.464

SSR-41	-1.000	0.650	0.825
SSR-82	-1.000	0.600	0.800
SSR-85	-1.000	0.581	0.790
SSR-90	-1.000	0.327	0.664
SSR-91	-1.000	0.663	0.831
MngSSR-14	-1.000	0.580	0.790
SSR16	-1.000	0.720	0.860
SSR17	-1.000	0.589	0.795
SSR22	-1.000	0.439	0.719
SSR24	-1.000	0.509	0.754
SSR26	-1.000	0.432	0.716
SSR29	-1.000	0.444	0.722
SSR34	-1.000	0.237	0.619
SSR36	-1.000	0.667	0.834
SSR37	-1.000	0.531	0.766
SSR39	-1.000	0.384	0.692
SSR49	-1.000	0.349	0.674
SSR83	-1.000	0.229	0.614
SSR84	-1.000	0.473	0.736
MNGSSR18	-1.000	0.806	0.903
MGDSSR2	-1.000	0.336	0.668
MGDSSR5	-1.000	0.529	0.764
MGDSSR6	-1.000	0.721	0.861
MGDSSR11	-1.000	0.421	0.710
MGDSSR17	-1.000	-0.911	0.045
MGDSSR22	-0.341	0.411	0.561
MGDSSR24	-1.000	0.651	0.826
Mean	-0.978	0.430	0.714

Genetic distance

Nei's genetic distance was used to estimate the genetic relationship between the 126 mango accessions from 15 populations. Nei's genetic distance showed broad variation among regions. The genetic similarity ranged from 0.096 to 1.191. The lowest genetic distance (Low diversity) was observed between Australia and USA while the highest genetic distance (high diversity) was observed between Sri Lanka and Tahiti, implying unique gene pools. These results highlight clear differentiation among geographic sources (Table 3).

Table 3. The average genetic distance between mango accessions from 15 populations

Australia	Brazil	India	IndoChina	Indonesia	Kenya	Malaysia	Israel	Oman	Philippines	SriLanka	Tahiti	Thailand	USA	Vietnam	
0.000															Australia
0.147	0.000														Brazil
0.119	0.158	0.000													India
0.286	0.391	0.430	0.000												IndoChina
0.262	0.323	0.328	0.507	0.000											Indonesia
0.598	0.617	0.608	1.129	0.695	0.000										Kenya
0.299	0.410	0.370	0.703	0.629	0.672	0.000									Malaysia
0.548	0.553	0.562	0.743	0.751	1.136	0.826	0.000								Israel
0.356	0.461	0.392	0.772	0.498	0.716	0.637	0.800	0.000							Oman
0.393	0.460	0.450	0.698	0.583	0.626	0.651	0.862	0.665	0.000						Philippines
0.667	0.811	0.665	0.920	0.826	1.172	0.740	0.946	0.919	1.155	0.000					SriLanka
0.558	0.545	0.538	0.924	0.598	1.062	0.826	1.037	0.928	0.999	1.191	0.000				Tahiti
0.096	0.186	0.133	0.441	0.310	0.555	0.301	0.506	0.287	0.409	0.668	0.633	0.000			Thailand
0.253	0.301	0.222	0.611	0.428	0.552	0.468	0.603	0.347	0.512	0.822	0.802	0.192	0.000		USA
0.188	0.234	0.223	0.387	0.315	0.657	0.487	0.606	0.409	0.567	0.775	0.729	0.212	0.316	0.000	Vietnam

Analysis of Molecular Variance (AMOVA)

An AMOVA analysis was achieved to elucidate the distribution of genetic variation among and within different mango accessions at a significance threshold of $P < 0.05$ (Figure 3). Results indicated that the most (87%) of molecular variation occurred within population, with lesser amount (13%) among populations, , which indicates mixing, gene flow, and shared ancestry rather than strict geographical separation.

Figure 3. Proportion of molecular variance among and within mango populations based on 55 SSR markers.

Cluster and Principal Coordinate Analysis (PCoA)

Principal Coordinate Analysis (PCoA) was performed to visualise allelic relationships across 126 mango accessions and to evaluate whether genetic clustering corresponded to geographic origin. Two

independent PCoA plots were generated, one based on population origin, and one based on individual genotype distribution, to increase resolution of diversity patterns.

The PCoA constructed at the population level (Figure 5) revealed moderate genetic dispersion among countries, with the first two axes explaining 53.83% of total variance (PC1 = 18.83%, PC2 = 35%). Populations from India, Brazil, Australia and Thailand overlapped extensively within the central coordinate space, suggesting shared genetic ancestry and historical exchange of material. Conversely, populations from Sri Lanka, Kenya and the Philippines appeared more isolated at the plot margins, indicating comparatively distinct genetic backgrounds or reduced introgression with other regions. Interestingly, Oman grouped close to several Asian and South American populations rather than forming an isolated cluster. This supports the notion that Omani mango germplasm has been influenced by historical introduction routes rather than evolving as an independent genetic lineage.

When individual genotypes were plotted (Figure 6), a broader distribution pattern emerged, reflecting high intra-population genetic variability, consistent with AMOVA results (87% within population variation). Despite general overlap among global cultivars, Omani accessions exhibited a semi-clustered pattern, reinforcing partial shared ancestry, yet also revealed scattered genotypes intermixing with Indian, Brazilian and Australian accessions. Distinct outlier positioning of cultivars from Sri Lanka, Tahiti, Kenya and the Philippines highlights the presence of geographically unique alleles and possible independent selection histories. These divergent accessions may represent valuable genetic reservoirs for breeding programs that aim to introduce new quality, yield or disease-tolerance traits.

Figure 4. Population-based PCoA showing the distribution of accessions according to country of origin.

Figure 5. Accession-level PCoA demonstrates individual genetic relationships among all 126 genotypes.

Cluster analysis of mango accessions

A dendrogram depicting the genetic relationships among different mango accessions was created using the UPGMA method, which assigns equal weight to each pair and calculates the average. Figure 4 displays a dendrogram that was created using a matrix of basic matching coefficients. This dendrogram clearly shows the presence of three main clusters. The first cluster (Cluster I) included cultivar Boribo from Kenya and cultivar Carabao Harbon from Philippines. The second cluster (Cluster II) has 2 subclusters in which one cluster contain accessions from Oman along with two accessions from USA (Haden) and Australia (Phoenix) which were clustered with Omani cultivars, and the second subcluster included 2 cultivars from Vietnam (Coconut and Xoai Tuong) and one cultivar from Indonesia (Kasturi). However, the third main cluster (Cluster III) contains all other mango cultivars from other origins. All clusters showed a mixture of poly-embryonic and mono-embryonic seed-type varieties in their cluster.

Figure 6. UPGM with arithmetic mean distance tree based on Nei genetic distances between 126 mango accessions using 55 SSR markers with bootstrap number for each node.

Estimated population structure among mangos cultivars

Population structure analysis using STRUCTURE v2.3.4 was performed for $K = 1-10$ under the admixture model. The ΔK method of Evanno et al. (2005) identified a strong peak at $K = 2$ (Figure 7), indicating that the 126 mango accessions form two major genetic sub-populations. The bar plot for $K = 2$ clearly separated Omani accessions (Sub-population II) from the majority of non-Omani genotypes (Sub-population I) (Figure 8).

Sub-population I (red) contained accessions predominantly from Indonesia (6), Brazil (2), India (3), Kenya (7), Malaysia (8), Sri Lanka (12), Occupied Island (9), Tahiti (13), USA (15), Vietnam (16), Thailand (14), Philippines (11), Indochina (5), and Australia (1). These accessions shared high membership probability within a single ancestry group, suggesting a largely interconnected genetic background. In contrast, Sub-population II (green) consisted mainly of genotypes from Oman (10), forming a distinct genetic cluster with minimal introgression from other regions. The clean separation of Omani accessions suggests the development of a semi-independent genetic lineage, likely shaped by local selection, geographical isolation, or region-specific allele retention. Although most non-Omani accessions grouped together, several genotypes displayed minor admixture signals, indicating historical gene exchange between Omani and foreign populations. This is consistent with PCoA and UPGMA outputs, which also support a shared ancestry between Oman and select Asian and South American germplasm.

Figure 7. The Evanno plot, derived from STRUCTURE HARVESTER, is used to detect the number of genetic clusters of mango accessions.

Figure 8. Estimated population structure for $K=2-4$ displayed with population Q-matrix. 10 runs at each K produced nearly similar population membership coefficients. The number in brackets represents the population number. Two sub-populations, or groups, are indicated by color; sub-population one (red) accessions from Indonesia (6), Brazil (2), India (3), Kenya (7), Malaysia (8), Sri Lanka (12), Occupied Island (9), Tahiti (13), USA (15), Vietnam (16), Thailand (14), Philippines (11), Indochina (5) and Australia (1) and sub-population two (green) accessions from Oman (10).

Discussion

The present study applied highly polymorphic SSR markers to evaluate genetic diversity within a globally sourced mango collection maintained in Oman. The detection of 706 alleles across 55 loci, averaging 12.8 alleles per marker, demonstrates a high level of genome-wide variation. Comparable or lower allele counts have been reported in previous studies from Taiwan, Mexico, India and Brazil (Chiang et al., 2012; Gálvez-López et al., 2009; Begum et al., 2013; Alves et al., 2016), whereas higher allelic richness was occasionally observed in elite cultivars or region-specific landrace panels (Vasugi et al., 2012; Ravishankar et al., 2017). The current dataset therefore represents one of the most diverse mango germplasm collections studied in the Arabian Peninsula.

Marker informativeness and heterozygosity

PIC values averaged 0.700, confirming the reliability of most markers for diversity assessment. High PIC values are indicative of multi-allelic loci and validate their suitability for genetic differentiation and germplasm fingerprinting. Observed heterozygosity exceeded expected heterozygosity at most loci, suggesting an over-representation of heterozygotes in the population. This pattern is consistent with mango's predominantly cross-pollinated reproductive biology, historical mass seed propagation, and ongoing orchard intermixing, which together promote allelic reshuffling and prevent inbreeding (Viruel et al., 2005; Schnell et al., 2006).

Genetic variance distribution and population structure

AMOVA results revealed that 87% of total variation resides within populations, with only 13% partitioned among populations. This indicates that genetic differences are predominantly found among individual accessions rather than between geographical groups. Such variance patterns are characteristic of long-domesticated, clonally propagated perennial fruit crops where recurrent gene flow and human-mediated movement mask regional separation (Miller and Gross, 2011).

This intrapopulation variation was further supported by STRUCTURE, UPGMA, and PCoA outputs, which did not strictly cluster accessions according to geographic origin. Instead, accessions from Asia, Australia, and the Americas frequently displayed admixture signals, while most Omani landraces clustered into a shared gene pool with a subset of foreign accessions. The grouping of Haden (USA), Phoenix (Australia), and Kasturi (Indonesia) within the Omani cluster suggests historical exchange of material, likely facilitated by maritime trade routes that linked Oman with mango-producing regions for centuries (Hammer et al., 2009).

High intrapopulation diversity presents a valuable opportunity for selection and genetic enhancement. The observed heterozygosity excess suggests that desirable traits, such as fruit quality, yield stability, or wilt disease tolerance, may exist in hidden combinations that can be explored through controlled hybridisation. Conversely, the lack of strong regional partitioning means that vegetative lineages have intermixed over time, likely diluting ancestral purity but enriching the available gene pool.

Conclusion

This study provides the most extensive molecular assessment of mango germplasm maintained in Oman, integrating 126 accessions from 15 global origins using highly informative SSR markers. The detection of 706 alleles, high PIC values, and strong heterozygosity levels reinforce the suitability of SSR markers for diversity estimation, genotype discrimination, and germplasm authentication in mango.

Population genetic parameters and AMOVA results indicated that the majority of genetic variation exists within populations rather than among them (87% vs. 13%), reflecting long-term outcrossing, historic germplasm exchange, and human-mediated distribution across regions. STRUCTURE and PCoA analyses confirmed the presence of two main ancestral gene pools, with Omani accessions forming a distinct but partially admixed cluster relative to international material. Accessions from Sri Lanka, Kenya,

Philippines, and Tahiti appeared genetically divergent, representing reservoirs of unique alleles that may be valuable for future breeding and trait improvement.

Collectively, these findings contribute to a clearer understanding of the molecular diversity landscape of mango in Oman and globally. The results provide strong justification for the targeted conservation of locally adapted cultivars, as well as for the incorporation of genetically distant accessions into breeding programs aimed at improving fruit quality, yield stability, environmental resilience, and wilt-disease tolerance. Future work integrating SNP-based genome scans, phenotypic trait evaluation, and association mapping will further deepen our understanding of trait–gene relationships and accelerate improvement pathways for this economically and culturally significant fruit crop.

Declarations

Author Contribution

Ali Al-Adawi: Writing – review and editing; Funding acquisition; Project administration. AL-Ghaliya Al-Mamari: Writing – review and editing; Data curation; Software and statistical analysis. Muna Al-Jabri: DNA extraction, genotyping, and laboratory analysis. Wafa Al-Shibli: DNA extraction, genotyping, and laboratory analysis. Muhammed Al-Jabri: Methodology and experimental work. All authors have read and approved the final manuscript.

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Figures

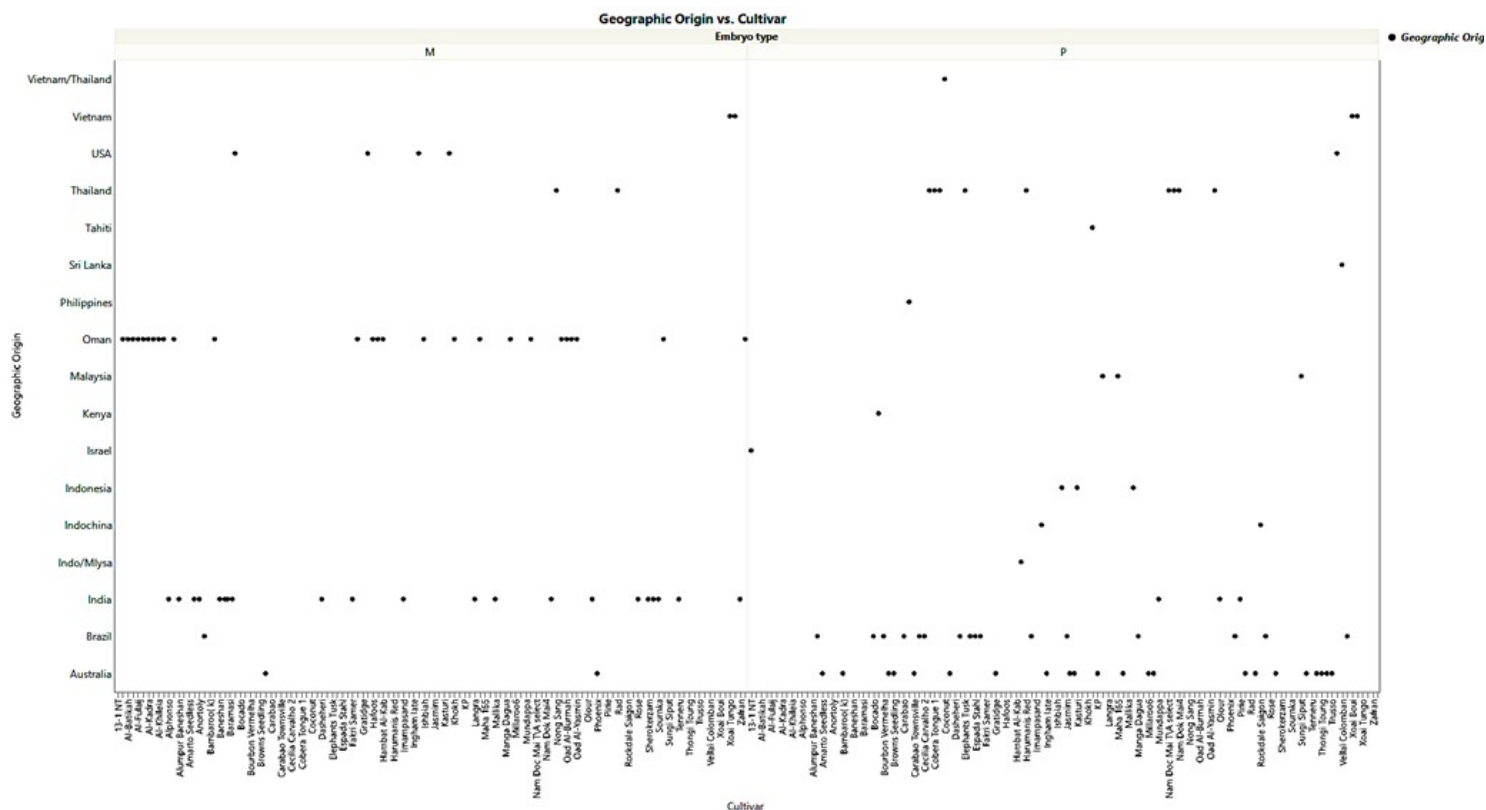


Figure 1

Mango growing in Oman and their accessions with code, Geographic origin, and embryo type for current study.

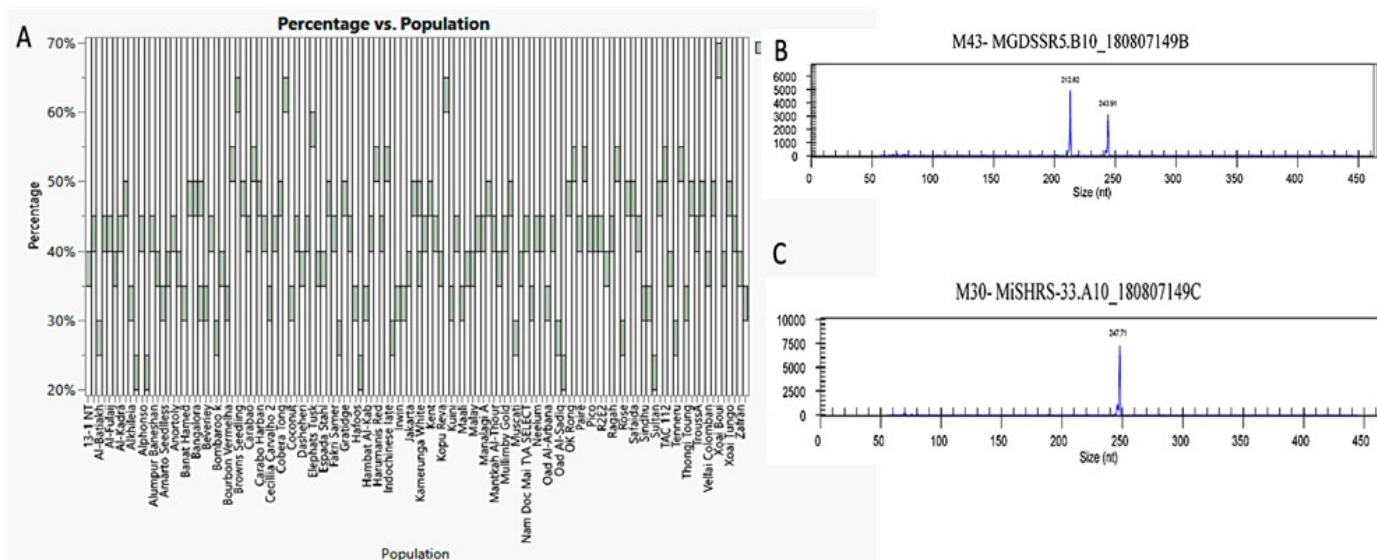


Figure 2

(A) The percentage of polymorphic loci in mango cultivars was determined using GenAlex. (B) Heterozygous allele showing 2 peaks for Dura accession using MGDSSR5. Scoring was performed using Beckman coulter software. The y-axis represents the maximum height of the peak, while the x-axis

represents the size of the peak in terms of base pairs. (C) Homozygous allele shows only 1 peak for Alphonso accession using MiSHRS-33. Scoring was performed using Beckman coulter software. The y-axis represents the maximum height of the peak, while the x-axis represents the size of the peak in terms of base pairs.

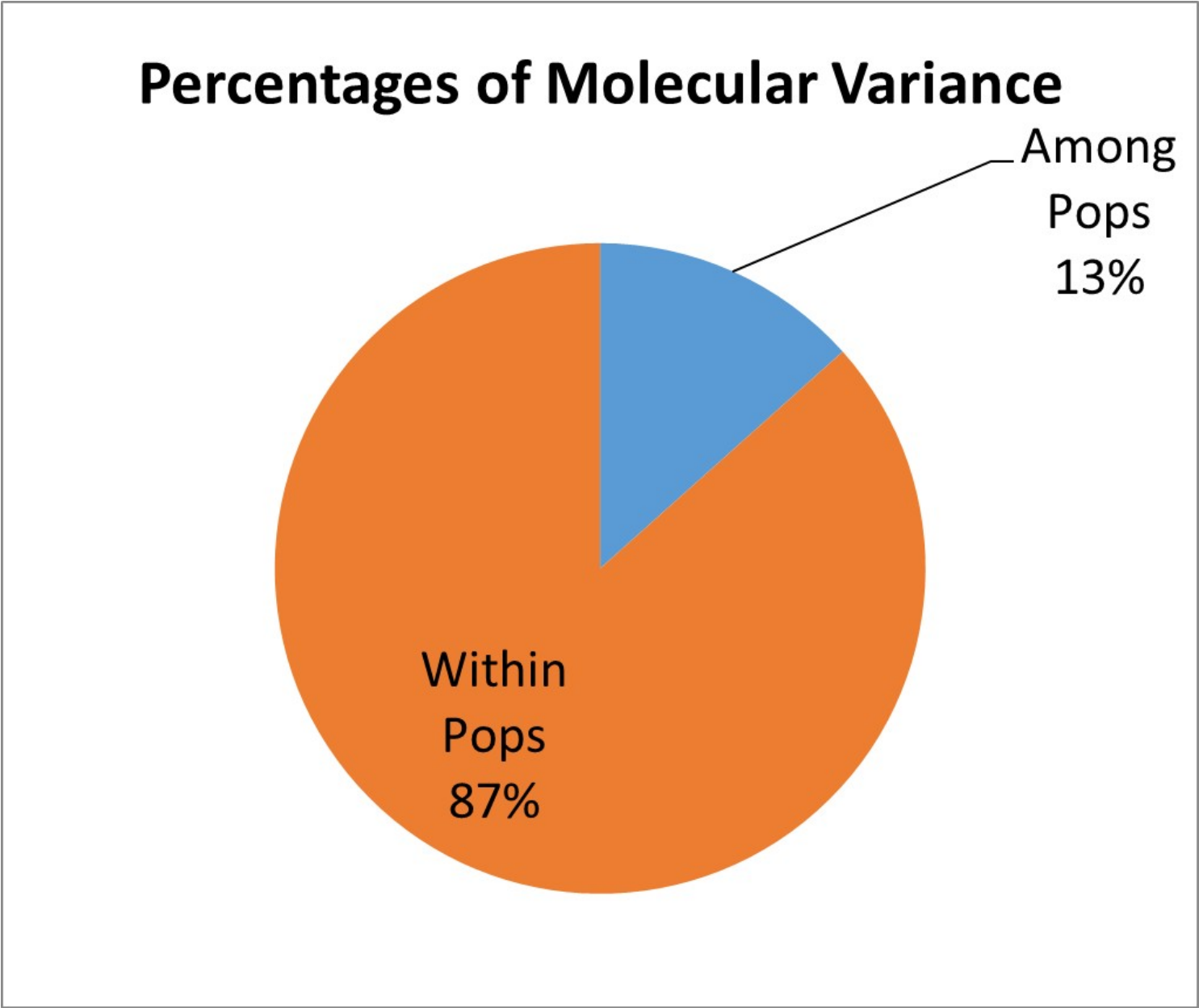


Figure 3

Proportion of molecular variance among and within mango populations based on 55 SSR markers.

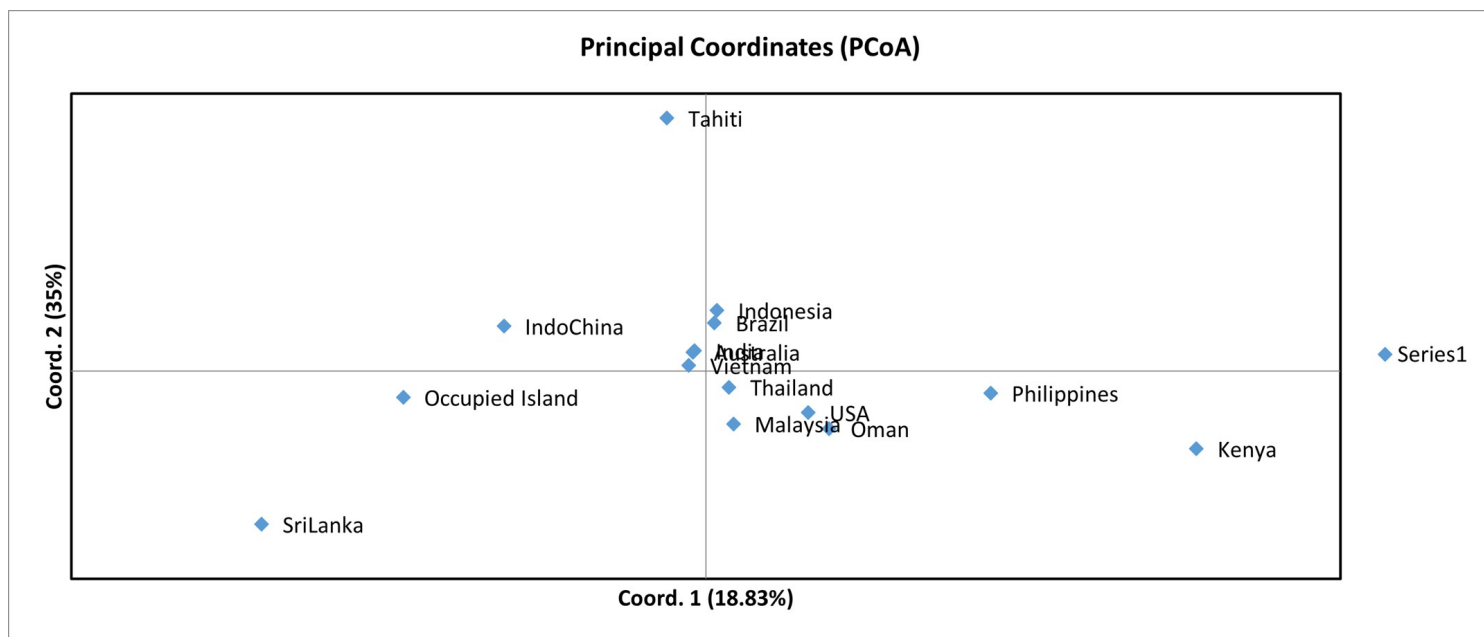


Figure 4

Population-based PCoA showing the distribution of accessions according to country of origin.

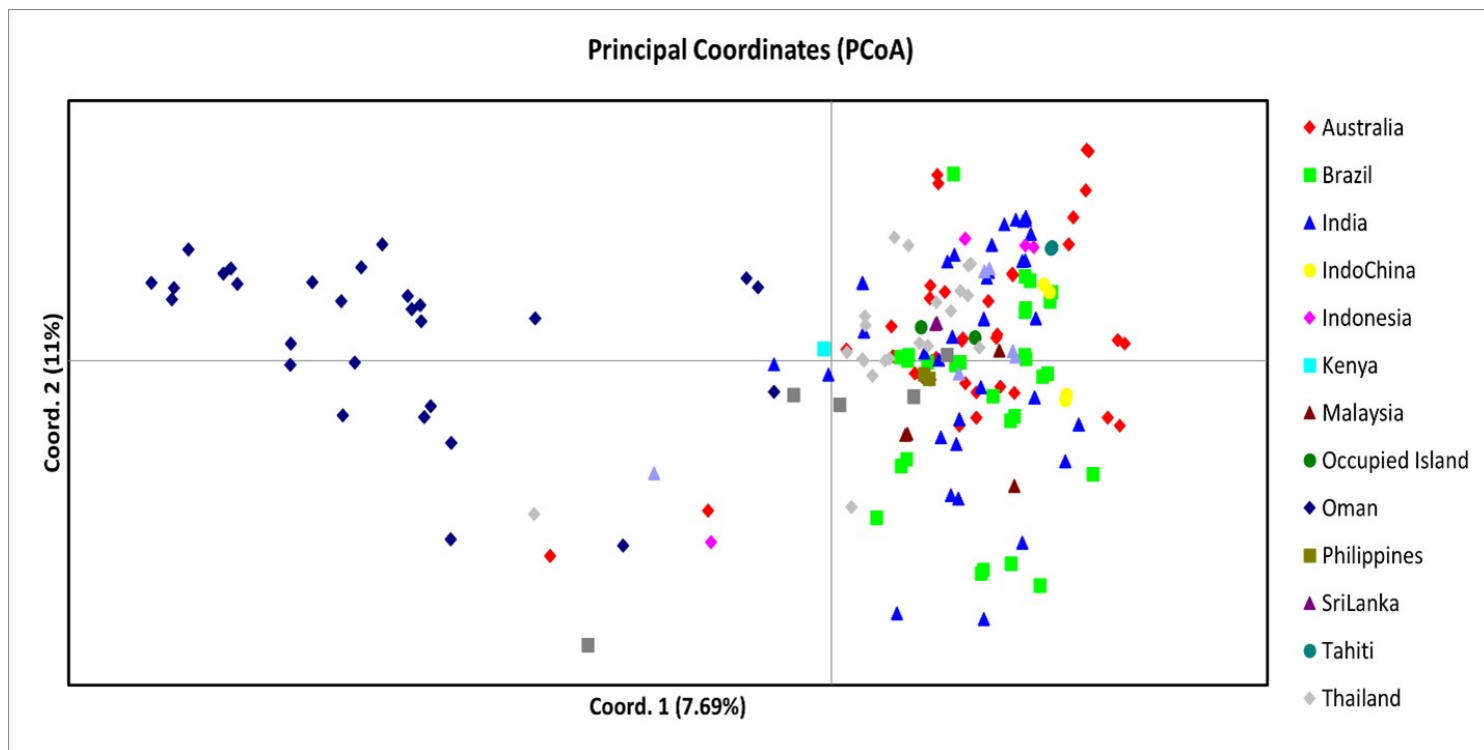


Figure 5

Accession-level PCoA demonstrates individual genetic relationships among all 126 genotypes.

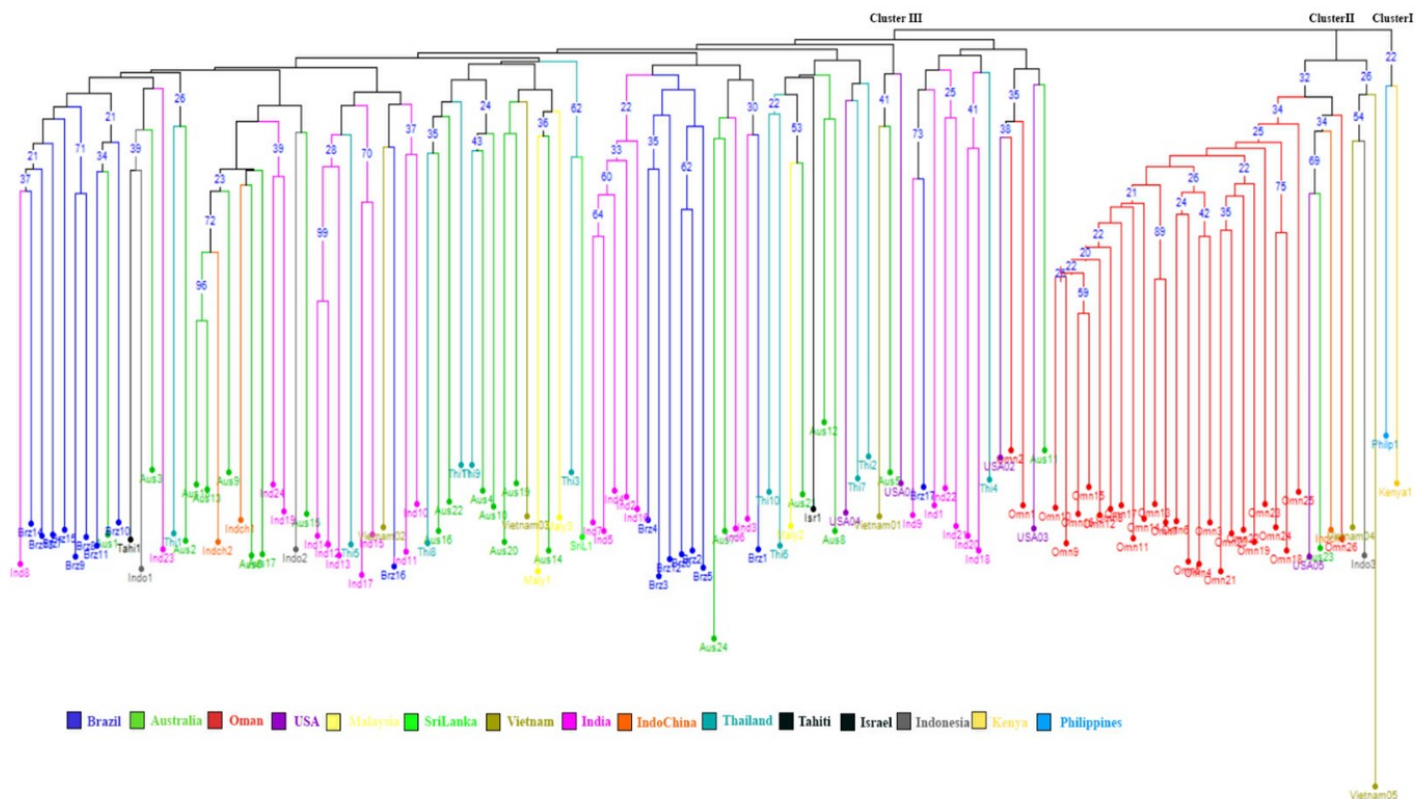


Figure 6

UPGM with arithmetic mean distance tree based on Nei genetic distances between 126 mango accessions using 55 SSR markers with bootstrap number for each node.

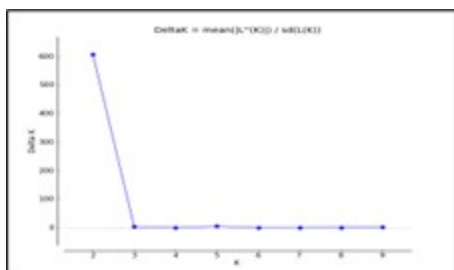


Figure 7

The Evanno plot, derived from STRUCTURE HARVESTER, is used to detect the number of genetic clusters of mango accessions.

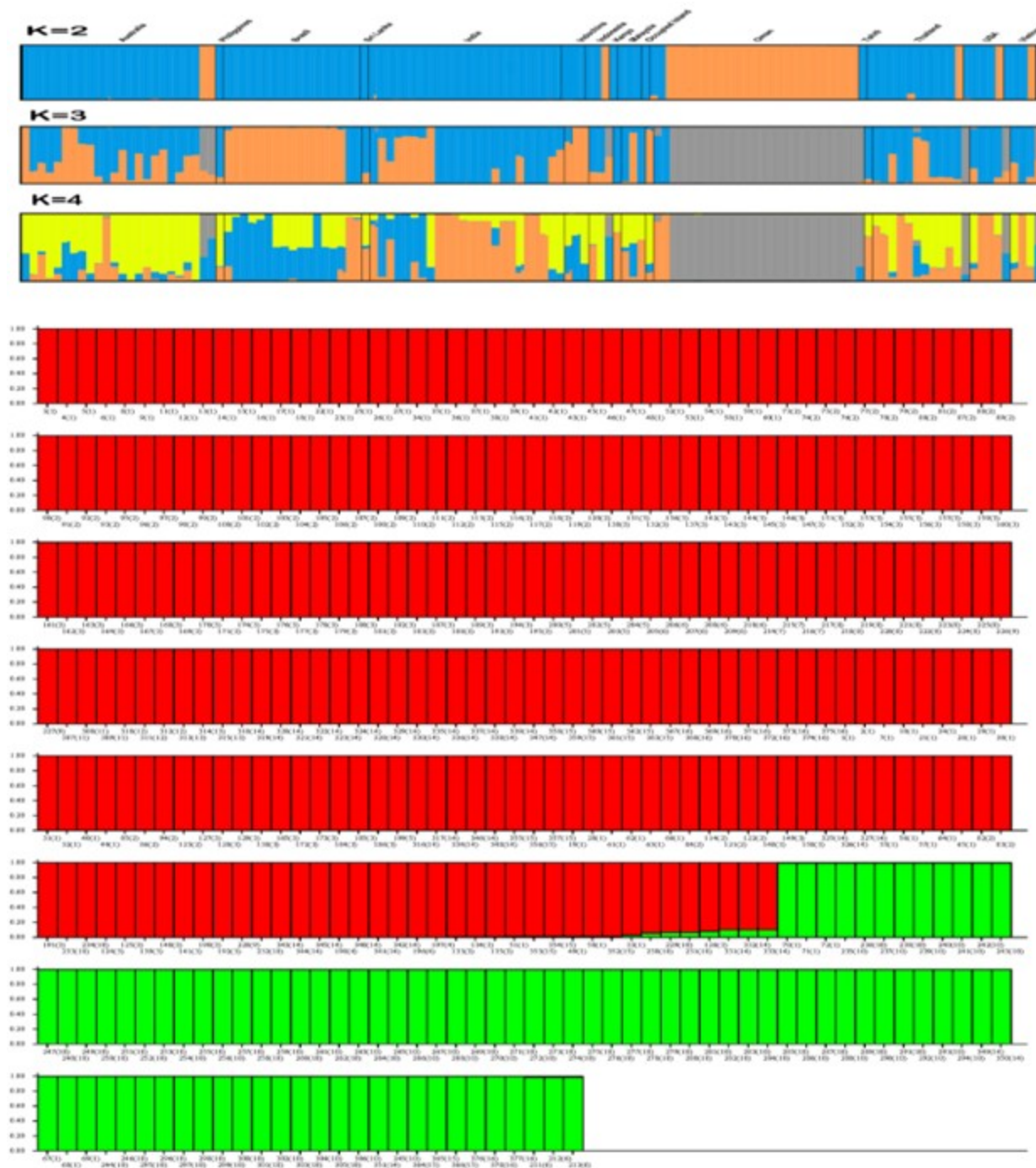


Figure 8

Estimated population structure for K=2-4 displayed with population Q-matrix. 10 runs at each K produced nearly similar population membership coefficients. The number in brackets represents the population number. Two sub-populations, or groups, are indicated by color; sub-population one (red) accessions from Indonesia (6), Brazil (2), India (3), Kenya (7), Malaysia (8), Sri Lanka (12), Occupied Island (9), Tahiti (13), USA (15), Vietnam (16), Thailand (14), Philippines (11), Indochina (5) and Australia (1) and sub-population two (green) accessions from Oman (10).