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Genetic variation among Iranian sesame (*Sesamum indicum* L.) accessions vis-à-vis exotic genotypes on the basis of morpho-physiological traits and RAPD markers

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Abstract

Characterization of overall genetic diversity is an important foundation in breeding for superior genotypes. For sesame (*Sesamum indicum* L.), an important oil seed crop, little is still known about genetic variability in many possible diversity hotspots, one of them postulated to be in Central Asia. We studied 27 sesame accessions, including 13 Iranian genotypes from 7 different locations and 14 exotic genotypes with wide geographical coverage. Variation among populations was characterized by 24 morphological, phenological and reproductive traits and by random amplified polymorphic DNA (RAPD) markers. Across genotypes, a factor analysis summarized the phenotypic traits best by six main factors, and important correlations were observed among key yield, phenological and morphological traits. A cluster analysis based on phenotypic traits separated the genotypes among four major groups and indicated high degree of phenotypic diversity in both the Iranian and the exotic genotypes. Genetic markers further underscored the high variability (Jaccard's similarity coefficient) of Iranian (0.39-0.92) compared with exotic (0.40-0.81) genotypes, consistent with our hypothesis of a diversity hotspot in Iran. A weak correlation was observed among the classifications based on phenotypic traits and RAPD marker data. The results revealed that RAPD markers can efficiently evaluate genetic variation in the sesame germplasm. These data collectively demonstrate large genetic variability among Iranian sesame genotypes that can be considered as a valuable gene pool for sesame breeding programs.

Keywords*: Sesamum indicum*, genetic diversity, phenotypic traits, RAPD markers, yield.
Abbreviations: 1000SM - 1000-seed mass; AFLP – amplified fragment length polymorphism; CL - capsule length; DFI - days to flowering initiation; DFT - days to flowering termination; LH - leaf hairiness; DMS - diameter of main stem; FC - flower colour; FP - flowering period; HFC - height to the first capsule; IMC - days to initial maturity of capsules; ISSR – inter simple sequence repeat; MP - maturity period; NMR - nuclear magnetic resonance; NB - number of branches; NCC - number of carpels per capsule; NCP - number of capsules per plant; NFLA - number of flowers per leaf axil; NSC - number of seeds per capsule; OC - seed oil content; PCA - principal coordinate analysis; P_G – growing season precipitation; PH - plant height; RAPD - random amplified polymorphic DNA; RP - reproductive period; SCC - seed coat colour; SMLB - seed mass on lateral branches; SMMS - seed mass on main stem; SYP - seed yield per plant; SRAP – sequence-related amplified polymorphism; SSR – simple sequence repeat; $T_{G,min}$ – growing season minimum temperature; $T_{G,max}$ – growing season maximum temperature; TMC - days to terminal maturity of capsules; UPGMA - unweighted pair group method with arithmetic mean.

Introduction

Sesame (*Sesamum indicum* L., Pedaliaceae), is one of the most important oil crops in warm temperate to tropical regions. Sesame seeds contain 45–60% oil and 25% protein, and compared to polyunsaturated oils from other crops such as flax, sesame oil has superior stability due to natural antioxidants sesamin and sesamolin, preserving the integrity of double bonds of unsaturated fatty acids (Brar and Ahuja, 1979). The beneficial effects of sesame oil on human health compared with saturated fats have been documented (e.g., Sankar et al., 2006). Sesame seeds also have multiple uses in food industry as ingredients, decorative elements and highly nutritious constituents of confections in bread, cakes, pastry and as halva. Despite the high nutritional value, health benefits and economic importance in many countries, sesame is largely ignored by plant breeders with a few exceptions (Bedigian, 2010a). Up to know, no agency affiliated with the Consultative Group on International Agricultural Research (CGIAR) is dedicated to research on sesame (Bedigian, 2003).The main challenges associated with sesame cultivation are drought and heat stress at certain periods of the growing season (Baydar, 2005; Grover and Singh, 2007; Mekonnen and Mohammed, 2009; Mensah et al., 2006) as well as pathogen attacks (Salehi and Izadpanah, 1992; Silme and Çağirgan, 2010). Furthermore, global change is predicted

to increase the severity of drought and heat stress in warm temperate to tropical areas with potentially large effects on yield (Ainsworth and Ort, 2010; Lobell et al., 2008; Lobell and Field, 2007). Thus, building on genetic diversity to find suitable varieties and breeding material for stressed conditions is of top priority to continue sesame cultivation in traditional areas. In addition, there has been interest in breeding sesame cultivars suitable for more temperate zones with cooler climates and longer days during the growing season (Weiss, 1983), but limited growing season length (Langham, 2007). Although the genus *Sesamum* contains 20 species of mainly African origin (Bedigian, 2010b), Bedigian's reciprocal crosses and phytochemical results (Bedigian et al., 1985), provide strong evidence that *S. indicum* was most likely domesticated on the Indian subcontinent. Archaeological evidence of sesame cultivation in India dates back at least as far as 2600 BC (Bedigian, 1998, 2000, 2003; 2004, 2010a; Bedigian and Harlan, 1986). In agreement with the domestication of sesame in India, a classical study has identified India, China, Central Asia and Near East as sesame diversity centres (Zeven and Zhukovsky, 1975). Initiated by Bedigian et al (1986), sesame diversity has been investigated using phenotypic markers such as morphological, physiological and phenological (morpho-physiological) traits (Banerjee and Kole, 2009; Bedigian et al., 1986; Bisht et al., 1998; Furat and Uzun, 2010; Morris, 2009) and isozyme patterns (Díaz et al., 1999; Isshiki and Umezaki, 1997), and a high level of variability in phenotypic characteristics within different sesame collections has been reported. However, geographic origin of sesame genotypes is not always strongly associated with the classification based on phenotypic traits (Bedigian et al. 1986). Because of environmental influences and complex genetic structure of many mopho-physiological traits (Banerjee and Kole, 2009), diversity analyses based only on morphological characters are prone to environmental bias. So far, genetic structure of only a few sesame traits has been revealed. Also, convergent modifications in plant structure and physiology complicate interpretations of phenotypic markers. Therefore, molecular markers have proved to be valuable tools in the characterization and evaluation of genetic diversity between species and among populations. In recent years, several studies have investigated the genetic diversity of sesame using DNA-based markers, including studies of world-based sesame collections (Ali et al., 2007; Laurentin and Karlovsky, 2006, 2007; Laurentin et al., 2008), and regional accessions from China (Zhang et al., 2007), India (Bhat et al., 1999; Kumar and Sharma, 2009), Korea (Kim et al., 2002), South-East Asia (Pham et al., 2009), and Turkey (Ercan et al., 2004). Although exotic genotypes have been included in studies of regional sesame diversity, Iranian accessions have seldom been included. To our knowledge, only in studies of Bedigan et al. (1986) and Morris (2009), four Iranian accessions were used in investigating the phenotypic variability among sesame worldwide germplasm accessions. This is surprising to us, given the potential sesame diversity hotspot in Central Asia. In this study, we investigated the genetic variation of Iranian sesame cultivars on the basis of morphological, phenotypic and reproductive (morpho-physiological) characteristics and genetic markers and compared this with the variability among exotic accessions, examining altogether 13 Iranian and 14 exotic accessions. We tested the hypothesis that the genetic variation among Iranian sesame genotypes is larger than commonly observed among local sesame accessions, consistent with the postulated sesame diversity hotspot. We also tested the hypotheses that diversity estimates based on two different sets of markers, morpho-physiological and molecular, are similar and correlated. Such a possible correlation between phenotypic and molecular markers would greatly simplify the use of molecular markers in breeding programs, but the relationships between phenotypic and molecular markers are not routinely examined.

Results

Variation in morpho-physiological characteristics among the genotypes

The analysis of variance revealed a statistically significant effect of genotype ($P < 0.01$) for the most quantitative traits studied except for capsule length. Among the genotypes, seed mass on main stem was the most variable trait (coefficient of variation, CV, of 41.7%, Table 3), while phenological traits, in particular, days to flowering termination (CV = 1.4%, Table 3), had low variability. Among the reproductive traits, seed oil content was the least variable (CV = 3.2%, Table 3). According to correlation analyses (Table 4), seed yield per plant was positively correlated with number of capsules per plant ($r = 0.79$, $P < 0.01$), seed mass of main stem ($r = 0.49$, $P < 0.01$), seed mass of lateral branches ($r = 0.45$, $P < 0.05$), diameter of main stem ($r = 0.41$, $P < 0.05$), and flower colour ($r = 0.47$, $P < 0.05$) (Table 4). No correlation was observed between seed coat colour and oil content (Table 4), a result that is in agreement with findings of El Tinay et al. (1976) and Bedigian (2010a). Among the Iranian genotypes, the highest seed yield per plant was found in NazOB (Sari). The average seed yield across all native genotypes was 0.94 t ha^{-1} with a range of 0.71-1.48 t ha^{-1} (Table 1). Within the exotic genotypes, the highest seed yield per plant was found in Is from Israel. Average seed yield across the exotic genotypes was 1.09 t ha^{-1} and the range was 0.68-1.76 t ha^{-1}. Factor analysis separated 21 quantitative variables into 6 factors that explained 74.1% of the total variance (Table 5). Plant height, number of capsules per plant, seed mass on lateral branches, seed yield per plant, days to terminal maturity of capsule, flowering period, maturity period and flower colour contributed to the first main factor that explained 25.7% of the total variation. Seed oil content had the greatest negative correlation (factor loading) with the first factor. Plant height to the first capsule, seed mass on main stem, and the number of flowers per leaf axil had the greatest positive loadings on the second factor, while the number of branches and maturity period had the largest negative loadings. These results collectively support the findings of the correlation analyses.

Segregation of genotypes on the basis of morpho-physiological traits

Cluster analysis gave insight into the relatedness of genotypes based on the morpho-physiological traits examined. Seed yield, branchiness, oil content, number of capsules per plant, maturation time, and plant height were the most effective in distinguishing the genotypes in this analysis. At an Euclidean distance of 12, the genotypes were divided into four groups (Fig. 3). Eight genotypes formed group A that was characterized by genotypes with single branch, medium seed yield, medium height, medium number of capsules per plant and early maturity. In this group, one distinct genotype (China) with low yield fell into a separate subgroup. Group B, composed of six genotypes, contained two subgroups with high yield. In this group, one genotype

Table 1. Origin and yield characteristics (average ± SE) of the studied sesame (*Sesamum indicum*) genotypes in the germplasm collection of the Oil Seed Crops Research Department, Seed and Plant Improvement Institute, Karaj, Iran. The origin of Iranian genotypes is shown in Fig. 1

ID No	Genotype	Site of collection	Oil content (%)	Yield (t ha^{-1})
1	Karaj1	Iran, Karaj	48.9±0.6	0.96±0.15
2	Yekta	Iran, Karaj	48.0±2.0	0.71±0.20
3	Oltan	Iran, Karaj	49.0±1.0	0.76±0.18
4	Moghan	Iran, Moghan	48.1±0.5	1.02±0.18
5	NazOB	Iran, Sari	46.4±1.4	1.48±0.18
6	NazMB	Iran, Sari	48.2±0.5	0.81±0.26
7	Borazjan2	Iran, Bushehr	49.5±1.5	1.07±0.20
8	Borazjan5	Iran, Bushehr	49.9±0.1	0.86±0.17
9	Darab14	Iran, Darab	50.9±0.6	1.13±0.29
10	Varamin37	Iran, Varamin	47.9±0.3	0.75±0.06
11	Varamin237	Iran, Varamin	49.4±1.4	0.87±0.11
12	Varamin2822	Iran, Varamin	50.1±0.4	1.10±0.19
13	Jiroft	Iran, Jiroft	51.1±1.1	0.71±0.12
14	Is	Israel	48.4±0.5	1.76±0.41
15	India	India	53.1±0.9	0.90±0.08
16	China	China	50.0±1.0	0.76±0.06
17	Yellowwhite	Pakistan	49.6±0.6	1.30±0.20
18	Panjab	Pakistan	50.0±1.0	1.01±0.22
19	Panama	Panama	51.4±0.3	1.03±0.10
20	Co-1	India, Tamil	50.0±2.0	1.13±0.17
21	Ts3	Pakistan	51.8±0.8	0.84±0.11
22	Tkg	Japan	48.1±0.5	1.11±0.14
23	J-1	Japan	51.8±0.5	0.68±0.18
24	Rt-54	India	50.2±0.2	1.33±0.17
25	India9	India	49.1±0.5	0.88±0.15
26	India12	India	47.5±0.6	0.98±0.16
27	India14	India	49.6±0.8	1.60±0.30

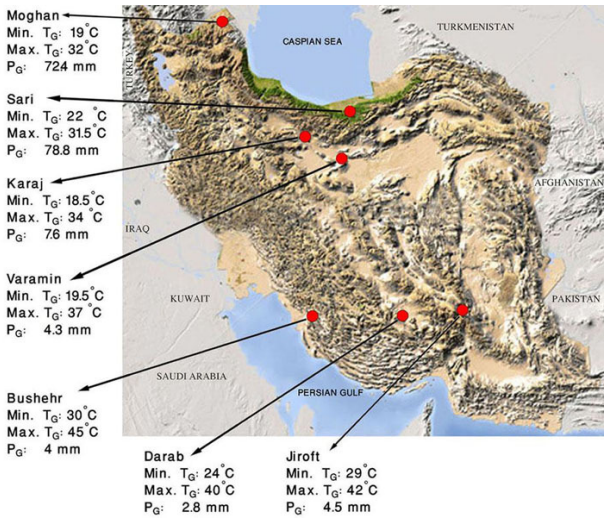

Fig 1. Location of the origin of studied sesame genotypes in Iran together with the key climatic drivers, temperature during the growing season between May and August (T_G), and precipitation during the growing season (P_G). Climatic data are average values for the period 2006-2010 (Iran Meteorological Organization, http://www.irimet.net).

(Is) with the highest yield among all genotypes was classified into a distinct subgroup. All genotypes of the group B had multi-branch stems, low oil percentage, medium height and high number of capsules per plant. Group C contained three genotypes from different regions of Iran (Karaj, Moghan and Varamin). This group included genotypes with low yield, high stem height, low oil content, medium 1000-seed mass and early maturity. Group D consisted of four genotypes from Iran and six genotypes from different countries. This group included genotypes with multi-branched stems with low or medium yield, medium height, high oil content and late maturity.

Genetic variability on the basis of RAPD analysis

Fifteen primers used displayed polymorphism among genotypes, resulting altogether in 111 polymorphic bands. The highest number of polymorphisms was observed with primers OPM-06 and OPA-20, while OPM-07 detected the lowest number of polymorphisms (Table 2). The number of

Table 2. Selected RAPD primers, and number of total and polymorphic bands observed in 27 studied sesame genotypes.

Numbers	Primers	Sequence, 5´ to 3´	Total no. of bands (n_T)	No. of polymorphic bands (n_P)	Polymorphism percentage ($n_P/n_T \times 100$)
1	OPA-02	TGCCGAGCTG	10	8	80
2	OPA-04	AATCGGGCTG	10	8	80
3	OPA-09	GGGTAACGCC	9	7	77.7
4	OPA-10	GTGATCGCAG	9	8	88.8
5	OPA-19	CAAACGTCGG	11	6	54.5
6	OPA-20	GTTGCGATCC	13	9	69.2
7	OPM-06	CTGGGCAACT	13	9	69.2
8	OPM-07	AGGCGGGAAC	7	4	57.1
9	OPM-18	TCAGTCCGGG	10	6	60
10	OPD-20	ACCCGGTCAC	11	8	72.7
11	OPB-10	CTGCTGGGAC	16	7	43.8
12	OPAC-09	AGAGCGTACC	13	8	61.5
13	OPF-09	CCAAGCTTCC	14	8	57.1
14	OPI-13	CTGGGGCTGA	12	7	58.3
15	OPQ-05	CCGCGTCTTG	13	8	61.5
Total			171	111	-
Mean			11.4	7.4	66.1

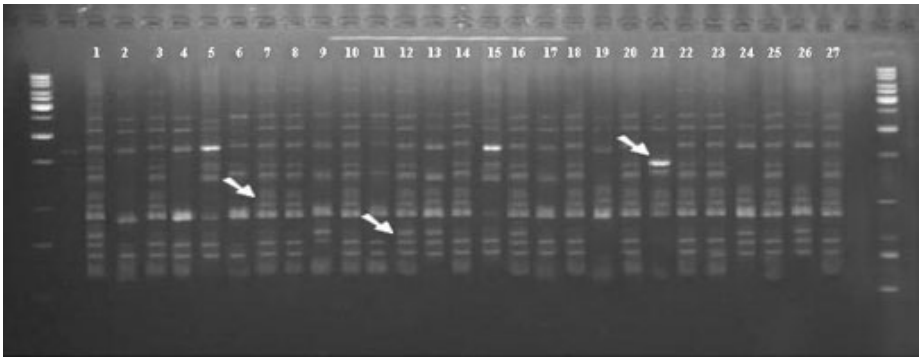

Fig 2. RAPD pattern of sesame genotypes amplified by decamer primer OPA-20. The numbers represent different sesame genotypes according to Table 1. The arrows show polymorphic bands

polymorphic bands ranged from four to 9 with an average of 7.4 per primer (Fig. 2, Table 2). The similarity matrix demonstrated highest similarity (0.92) among two Iranian genotypes Oltan and Moghan. These two genotypes were similar according to morpho-physiological traits as well. The lowest similarity (0.39) was between the genotypes NazMB from Iran and Panama from South America. The similarity coefficient ranged between 0.39 and 0.92 among the Iranian genotypes, and between 0.40 and 0.81 among the exotic genotypes, indicating that a similar range of variability was present in the native and exotic genotypes. The UPGMA dendrogram fitted the similarity matrix well and provided a relatively good representation of relationships among the genotypes in the clusters. At a similarity level of 0.52, the genotypes were divided into five sub-clusters containing two to eleven genotypes (Fig. 4). Four genotypes, two from Iran and two from other countries formed group A. Group B was the largest group with 11 genotypes, 6 genotypes from Iran and 5 from other countries. Group C consisted of five exotic genotypes, with two genotypes from India and three from other countries. Out of five genotypes in cluster D, three were from central provinces of Iran, one from northern part of Iran and one from India. Cluster E consisted of only two genotypes, a genotype from Sari, Iran and the other from Israel. The principal coordinate analysis (PCA) with the 15 random RAPD primers (Fig. 5) indicated that the first two principal coordinates, PCA1 and PCA2, explained 14.5% and 10.6% of the variation, respectively. According to the Mantel test, there was a weak correlation (r^2 = 0.22, P < 0.05) between the genotype classifications based on RAPD markers (genetic distances) and morpho-physiological traits (phenotypic distances).

Discussion

Genetic diversity of sesame based on morpho-physiological characteristics

Morpho-physiological characteristics revealed a high level of polymorphism among Iranian and exotic sesame accessions. The variations in the Iranian sesame collection include differences in plant habit, flower colour, capsule characteristics, number of capsules per plant, number of seeds per capsule, and yield per plant. These findings support previous observations of strong variability in these traits among sesame genotypes (Bedigian, 2010a, b; Bedigian et al., 1986; Ercan et al., 2002). The dendrogram based on morpho-physiological traits consisted of four main genotypes

Table 3. Studied morphological characteristics, and phenological and reproductive traits in 27 sesame accessions: average ± SE, coefficient of variation (CV) and range

Number	Character	Acronym	Unit	Average ± SE	CV (%)	Range
	Morphological traits					
1	Number of branches	NB	-	3.20±0.40	24.9	1 - 7.65
2	Plant height	PH	cm	136.7±2.7	8.0	87 – 182
3	Height to the first capsule	HFC	cm	83.1±2.6	11.0	25.4 – 117
4	Diameter of main stem	DMS	mm	1.53±0.05	20.7	0.96 - 4.06
5	Capsule length	CL	cm	2.81±0.10	8.5	1.44 - 3.55
6	Number of carpels per capsule	NCC	-	4.07±0.07	-	4 – 8
7	Number of seeds per capsule	NSC	-	70.0±1.0	8.2	50.2 - 98.6
8	Number of capsules per plant	NCP	-	100.0±6.0	27.6	34.2 – 241.6
9	Number of flowers per leaf axil	NFLA	-	1.80±0.20	-	1 – 3
10	Flower colour*	FC	-	2.80±0.20	-	1 – 5
11	Leaf hairiness*	LH	-	2.10±0.20	-	1 – 3
12	Seed coat colour*	SCC	-	3.30±0.20	-	1 – 6
	Phenological traits					
13	Days to flowering initiation	DFI	days	47.7±0.9	2.80	38 – 66
14	Days to flowering termination	DFT	days	100.0±2.0	1.43	82 – 128
15	Flowering period	FP	days	52.5±1.7	4.10	36 – 81
16	Days to initial maturity of capsules	IMC	days	107.4±1.3	1.80	92 – 121
17	Days to terminal maturity of capsules	TMC	days	121.2±1.8	1.60	101 – 143
18	Maturity period	MP	days	13.8±1.9	17.5	1 – 41
19	Reproductive period	RP	days	73.5±1.5	3.50	57 – 96
	Reproductive traits					
20	Seed oil content	OC	%	49.5±0.3	3.15	44.01 - 54.68
21	Seed yield per plant	SYP	g	14.2±0.7	32.4	4.27 - 35.26
22	Seed mass on main stem	SMMS	g	9.7±0.8	41.7	1.53 - 27.11
23	Seed mass on lateral branches	SMLB	g	6.8±0.7	19.8	0 - 16.56
24	1000-seed mass	1000SM	g	2.99±0.06	6.6	1.62 - 3.76

*- Qualitative traits, Flower colour: 1, white; 2, white with pink shading; 3, pink; 4, purple; 5, dark pink with purple spots. Leaf hairiness: 1, no hair; 2, medium hair; 3, hairy. Seed coat colour: 1, white; 2, beige; 3, light brown; 4, dark brown; 5, brown to black; 6, black.

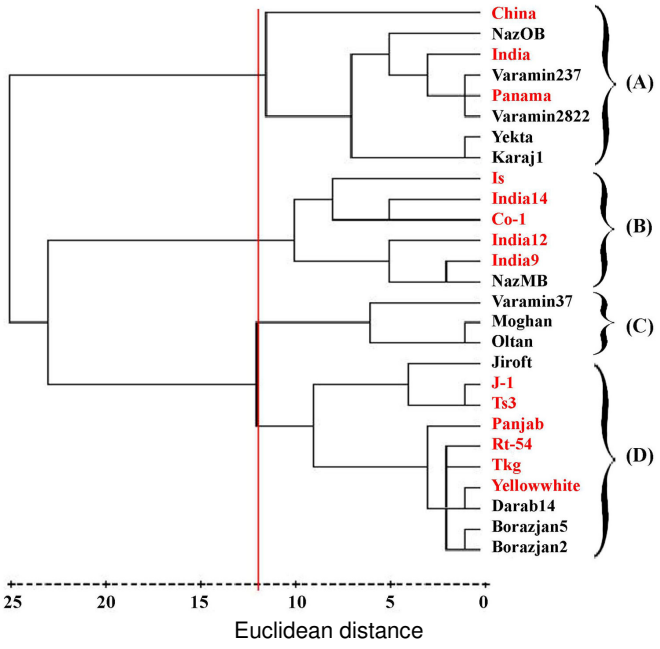

Fig 3. Dendrogram of clustering of 27 studied sesame genotypes based on phenotypic traits. Names in black font correspond to native genotypes and in red to exotic genotypes (Table 1 for studied sesame genotypes, Fig. 1 shows the origin of native genotypes).

(Fig. 3). However, in this classification, as well as according to PCA analyses (Fig. 5), native and exotic genotypes were not always clearly separated. This overlap among the genotypes contrasts somewhat the earlier observations based on morpho-physiological traits. Bedigian et al. (1986) found that the 4 Iranian accessions they examined clustered together with some accessions from Iraq, Turkey and Israel. On the other hand, overlapping of some Indian and some Turkish genotypes, and an overall diffuse representation of Chinese genotypes across all clusters was observed in their study (Bedigian et al. 1986). Therefore, we concur, since geographic origin of genotype was not always strongly associated with classification based on morpho-physiological characteristics of genotypes, as in our study.

Molecular markers to study sesame genetic diversity

Thus far, a variety of PCR-based genetic markers have been employed to reveal genetic polymorphisms. Previous studies on sesame were based on RAPD (Bhat et al., 1999; Ercan et al., 2004; Pham et al., 2009; Salazar et al., 2006), AFLP (amplified fragment length polymorphism) (Ali et al., 2007; Laurentin, 2007; Laurentin and Karlovsky, 2006; 2007; Laurentin et al., 2008), ISSR (inter-simple sequence repeat) (Sharma et al., 2009; Kim et al., 2002), SSR (simple sequence repeat, also called microsatellite) (Zhang et al., 2007), and SRAP (sequence-related amplified polymorphism) (Zhang et al., 2010) markers. Various methods differ in requirement for a priori knowledge of genome sequences, amount of DNA and the number of chemical steps needed to get the final result (Garcia-Mas et al., 2000; Garcia et al., 2004; Gzyl et al., 2005). While SSR markers are very effective in revealing polymorphisms (Powell et al., 1996), and require small amounts of DNA, sequence information is needed for primer design (Sun et al., 1998), and thus, often genetic diversity can be studied only on the basis of a limited number or markers (Agarwal et al., 2008). For AFLP markers, certain former knowledge about genome sequence is not needed, but this technique is relatively expensive as multiple chemical steps are needed until polymorphisms can be detected. In the case of RAPD, a large number of polymorphic markers can be obtained with relative ease from minute amounts of genomic DNA without prior knowledge of sequence information (Williams et al., 1990). Although the early studies have reported poor reproducibility of RAPD markers (Devos and Gale, 1992), further it has been demonstrated that use of optimized conditions and rigorous protocols results in consistent and reproducible RAPD results (Salem et al., 2007; Yu et al., 2004). In different organisms, comparisons among various marker systems have demonstrated that both RAPD and AFLP markers resulted in similar classifications of genotypes (Divakaran et al., 2006; Garcia-Mas et al., 2000; Gzyl et al., 2005). In sesame, RAPD markers have been able to discriminate among all the sesame accessions (Bhat et al., 1999; Pham et al., 2009; Salazar et al., 2006), indicating that RAPD markers are suitable for characterizing sesame germplasm. Given this, we used RAPD markers in our study and only reproducible bands were analysed.

Genetic diversity of sesame genotypes based on molecular markers

The molecular data showed that the average percentage of polymorphism across all primers was 66.1% and the average amount of polymorphisms for each primer was 7.4 (Table 2). This degree of polymorphism is wholly acceptable to investigate the genetic variation among the genotypes, and this degree is similar to other studies using RAPD markers (Bhat et al., 1999; Ercan et al., 2002). The coefficient of similarity based on molecular markers ranged from 0.39 to 0.92 in native and from 0.40 to 0.81 among exotic genotypes, demonstrating that a similar degree of genotypic variability was observed among the native genotypes coming from a limited area and exotic genotypes coming from a wide geographic range. Compared with other studies conducted with RAPD markers, the variability observed in our study is higher than that in Indian genotypes studied by Kumar and Sharma (2009), in South-East Asian sesame genotypes (Pham et al., 2009), and in Sudanese genotypes (Abdellatef et al., 2008). However, the variability in our study is lower than in a more extended study of Indian genotypes (Bhat et al., 1999) and in Venezuelan genotypes (Salazar et al., 2006), where exceptional variability was reported (Table 6 for comparisons with literature data). Altogether, this evidence indicates high genetic variability in our study. Based on fully fertile reciprocal crosses and evidence from phytochemical comparisons of lignan profiles, it was suggested that the Indian subcontinent is the center of sesame domestication (Bedigian, 1988, 1998, 2000, 2003; Bedigian et al., 1985), and high diversity of molecular markers has been suggested to support this (Bhat et al., 1999). Thus, high diversity observed for Iranian sesame accessions in our study is consistent with the postulated secondary sesame diversity hotspot in Central Asia. The high level of polymorphism according to RAPD markers (Fig. 4) indicates a wide and diverse genetic base of the studied sesame germplasm. Sampling areas and plant characteristics such as types of reproduction, breeding behaviour and generation time are some of the important parameters that determine the level of genetic diversity among the genotypes. High degree of outcrossing, up to 60% in some rare instances, described in sesame (Brar and Ahuja, 1979; Yermanos, 1980) may be partially responsible for this high level of genetic variability.

Comparison of genetic variability among studied Iranian and exotic genotypes

Distribution of genetic diversity for a given species is dependent on evolutionary and breeding factors, species ecology and geographical human factors (Ramanatha and Hodgkin, 2002). In sesame, high local diversity is associated with cross-pollination, depending on the presence of pollinating insects at flowering time (Bhat et al., 1999). However, large-scale diversity depends more strongly on human factors. Migration and trade have influenced sesame distribution; as a result, continuous gene flow can take place among cultivars from different geographical regions. In our study, the relationship between genetic distance and geographical distance was complex. While there was a tendency of some Iranian genotypes to be more frequent in some of the clusters (e.g., clusters A and C, according to morphological classification and clusters B and D, according to molecular markers), some of the Iranian genotypes were forming clusters with exotic genotypes and vice versa. For example, Borazjan2, Borazjan5 and Darab14 collected from south of Iran (Fig. 1), grouped in one cluster, so there clearly was evidence of certain tendency of Iranian genotypes to be clustered together (Fig. 4 and 5). On the other hand, based on morpho-physiological data, genotypes India9, India12 and India14 of Indian origin, were categorized in one group, whereas, based on molecular data, genotypes India9 and India12 were in one group and genotype India14 was

Table 4. Correlation coefficients among the key morphological, phenological and reproductive traits (Table 3 for acronyms) for the sesame accessions

	NB	DMS	NCP	CL	NSC	PH	SMLB	HFC	1000SM	OC	SMMS	SYP	*FC*	NFLA	NCC	RP
SMLB	0.556**	0.012	0.686**	0.004	-0.052	0.341										
HFC	-0.316	0.301	0.387*	0.257	0.112	0.614**	0.284									
1000SM	0.436*	-0.031	-0.249	0.233	0.134	-0.064	0.119	-0.239								
OC	0.258	0.038	-0.255	-0.177	0.05	-0.246	-0.221	-0.692**	0.248							
SMMS	-0.308	0.322	0.129	0.028	0.187	-0.02	-0.481*	0.185	-0.244	0.054						
SYP	0.272	0.411*	0.788**	0.021	0.016	0.175	0.450*	0.341	-0.081	-0.092	0.493**					
FC	0.486*	0.097	0.631**	0.016	-0.093	0.028	0.691**	0.166	0.067	-0.113	-0.192	0.468*				
NFLA	-0.721**	0.189	0.145	-0.145	-0.261	-0.058	-0.227	0.136	-0.658**	-0.184	0.194	0.019	-0.13			
NCC	-0.231	-0.05	-0.252	-0.277	0.327	0.176	-0.231	0.151	-0.201	0.076	0.101	-0.2	-0.163	-0.163		
FP	-0.027	0.36	0.431*	-0.13	0.138	0.402*	0.324	0.425*	-0.424*	-0.253	-0.025	0.228	0.523**	0.18	0.24	
RP	0.510**	0.134	0.303	0.039	0.063	0.207	0.565**	-0.077	0.078	0.133	-0.454*	0.205	0.419*	-0.281	-0.126	
MP	0.409*	0.172	0.076	0.316	-0.13	0.274	0.511**	-0.02	0.205	0.163	-0.576**	0.009	0.237	-0.223	-0.265	0.689**
SCC	0.352	0.26	-0.08	0.217	-0.046	0.174	-0.076	-0.13	0.31	0.003	0.001	0.054	-0.198	-0.362	-0.284	0.182

* - significant at $P < 0.05$, ** - significant at $P < 0.01$. For quantitative traits, Pearson pairwise correlation coefficients were calculated. For correlations between quantitative and qualitative traits and for qualitative traits, Spearman rank correlation coefficients were used.

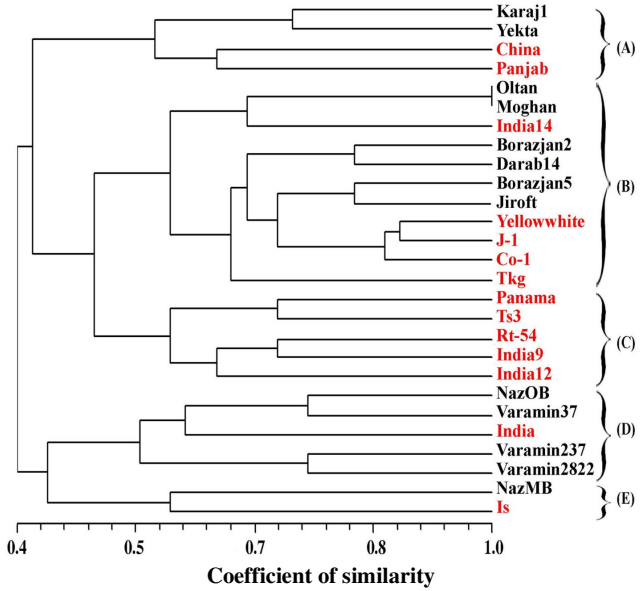

Fig 4. UPGMA cluster analysis of 27 studied sesame genotypes based on RAPD data. Black font refers to native genotypes and red to exotic genotypes (Table 1 for all sesame genotypes, Fig. 1 for geographic location and origin of native genotypes).

clustered with Iranian genotypes in another group. Perhaps, in this case, some of the Iranian genotypes originated from Indian genotypes and vice versa. This lack of strong association between geographical distribution and classification based on molecular markers in sesame has been observed also in other studies (Kim et al., 2002; Laurentin and Karlovsky, 2006; Pham et al., 2009), and may reflect exchange of sesame germplasm among widely separated locations (Kim et al., 2002; Pham et al., 2009).

Correlations between morpho-physiological and genetic markers

Generally, morpho-physiological and molecular data are complementary to each other. Morpho-physiological data provide key information on plant traits, while molecular data provide information on genetic basis of these traits. In our study, the comparison of genotype classifications based on the morpho-physiological traits and RAPD markers using Mantel test showed that there was only a weak correlation among the two classifications. Analogously, a poor correlation between molecular and morphological markers in sesame was observed by Ercan et al (2004) and Bhat et al (1999). Nevertheless, in our study, a weak correlation between the two different means of clustering suggests certain similarities. For example, similar to morpho-physiological clustering, genotypes Karaj1 and Yekta were clustered together in one group according to molecular data, although two exotic genotypes, Panjab and China, were also in this group. Both morpho-physiological and molecular clustering positioned Iranian genotypes 3 and 4 closely together. Furthermore, genotype 14 (Is) was classified as very distinct according to both morpho-physiological traits and genetic markers, although, according to genetic markers, it clustered together with Iranian genotype 6 (NazMB). This overall low correlation between two means of clustering can have different causes, such as convergent evolution and complex genetic structure of traits, resulting in environmental effects on trait expression. At any rate, this poor correspondence suggests that firm evolutionary conclusions can not be based on morphological traits in sesame, at least for the genotypes studied here. Also, this limited linkage of molecular markers and phenotypic traits indicates that the molecular markers can not yet be effectively included in sesame breeding programs. In a similar manner, Laurentin and co-workers (2008) studied the relationship between genetic and metabolic diversity in sesame using a combination of high-performance liquid chromatography (HPLC) and amplified fragment length polymorphism (AFLP) and observed major differences in the patterns of diversity at the genomic and metabolic levels. While the molecular markers can highlight the potential genotypic diversity, more genetic work is necessary to gain insight into the expression of phenotypic traits with complex genetic background (Fleury et al., 2010). Nevertheless, among the traits evaluated, seed yield per plant, height to the first capsule, flowering period, and number of capsules showed high correlation with molecular data, providing encouraging evidence that for traits with less complex genetic background, molecular markers can be effective in sesame breeding.

Materials and methods

Plant material

Twenty seven sesame genotypes, consisting of 13 Iranian genotypes from key Iranian sesame cultivation areas (Figure 1) and 14 exotic accessions from widely disparate world regions (Table 1) were obtained from the germplasm collection of the Oil Seed Crops Research Department, Seed and Plant Improvement Institute, Karaj, Iran. The Iranian sesame cultivation regions were characterized by wide variation in growing season minimum ($T_{G,min}$) and maximum temperatures ($T_{G,max}$), and in particular, in precipitation (P_G, Figure 1).

Morphological, phenotypic and reproductive traits

Phenotypic traits in all genotypes were studied at the experimental field of the Faculty of Agriculture, Tehran University, Karaj, Iran (35° 48' N, 51° 00' E, elevation 1321 m) between mid-June (seed planting) and August (plant harvesting) 2005. During this period, $T_{G,min}$ of 18.5 °C; $T_{G,max}$ of 34°C and P_G of 7.6 mm were recorded. Experiments were designed in a randomized complete block with three replicates. Each replicate consisted of 27 plots, and each plot had five rows of 4 m length with 0.7 m intercropping distance. Altogether 24 morpho-physiological traits, based on sesame descriptors (IPGRI and NBPGR, 2004) and known to exhibit strong variation among genotypes (Bedigian et al., 1986; Langham, 2007; Mekonnen and Mohammed, 2009) were investigated and analyzed. Quantitative traits studied were plant height (PH, cm), number of branches (NB), height to the first capsule (HFC, cm), diameter of main stem (DMS, mm), capsule length (CL, cm), number of flowers per leaf axil (NFLA), number of carpels per capsule (NCC), number of seeds per capsule (NSC), number of capsules per plant (NCP), days to flowering initiation (DFI, days since planting), days to flowering termination (DFT, days since planting), flowering period (FP, days), days to initial maturity of capsules (IMC, days since planting), days to terminal maturity of capsules (TMC, days since planting), maturity period (MP, days), reproductive period (RP, days), seed oil content (OC, %), seed yield per plant (SYP, g), seed mass on main stem (SMMS, g), seed mass on lateral branches (SMLB, g) and mass of 1000 seeds (1000SM, g). In addition, three qualitative traits - seed coat colour (SCC), flower colour (FC), and leaf hairiness (LH) - were included in the analysis. In the case of qualitative traits, the qualitative coding of traits was converted to a numerical ranking. For colour, the ranking evaluated the trait from lightest to darkest, i.e., flower colour was ranked, from white to dark purple, and seed coat from white to black (see Table 3 for complete description). Hairiness ranking was assessed from glabrous to strongly hairy. Ten plants in the mid-row of each plot were chosen randomly for in situ measurements. After ripening, the seeds were harvested, dried at 25 °C for at least 72 hrs, and seed yield per plant, seed mass on main stem, seed mass on lateral branches and 1000-seed mass were estimated. The latter characteristic was estimated using the dry mass of 200 seeds. Yield per unit ground area was calculated based on average seed mass per plant, and plant density, and expressed in t ha^{-1}. Seed oil content for each plot was estimated as average of two measurements by nuclear magnetic resonance (NMR, Avance, 300 MHz, Bruker, HB, Germany) at the Oil Seed Crops Research Department Laboratory, Seed and Plant Improvement Institute, Karaj, Iran. For these measurements, a random seed sample of 3.24 ± 0.09 g was used (Conway and Earle, 1963).

Molecular markers

Young healthy three-week-old leaves from the apical plant part were harvested for DNA extraction. Total genomic DNA was isolated using the CTAB method (Porebski et al., 1997). PCR reactions were carried out in a 25 µl volume containing

Table 5. Eigenvalues, cumulative variances and factor loadings with key phenotypic traits for six factors derived from the factor analysis

Statistic	Factor					
	1	2	3	4	5	6
Eigenvalue	5.402	3.945	2.599	2.141	1.722	1.216
Cumulative variance (%)	25.725	38.51	49.89	60.1	68.3	74.09
Variable	Factor					
	1	2	3	4	5	6
	Factor loading					
Plant height	0.608	0.176	-0.027	0.737	-0.272	0.194
Number of branches	0.361	-0.768	-0.616	-0.217	-0.081	-0.285
Height to the first capsule	0.464	0.545	0.087	0.56	-0.153	-0.565
Diameter of main stem	0.474	0.331	0.157	0.803	0.122	0.280
Capsule length	0.128	-0.052	-0.073	0.100	-0.243	-0.221
Number of flowers per leaf axil	0.017	0.661	0.914	-0.029	0.051	-0.365
Number of capsules per plant	0.749	0.190	0.086	0.153	-0.034	-0.114
Number of seeds per capsule	0.066	-0.046	-0.412	0.636	0.183	0.395
Flower colour	0.681	-0.140	-0.11	-0.01	0.138	-0.141
Days to flowering initiation	0.331	0.244	0.787	0.046	0.228	-0.217
Days to flowering termination	0.749	0.378	0.559	0.550	0.147	0.423
Flowering period	0.727	0.329	0.247	0.653	0.053	-0.420
Days to initial maturity of capsules	0.095	0.283	0.101	0.02	0.935	-0.325
Days to terminal maturity of capsule	0.68	-0.353	0.21	0.17	0.27	-0.253
Maturity period	0.561	-0.511	0.126	0.143	-0.369	-0.311
Oil content	-0.293	-0.429	-0.112	-0.077	-0.110	0.420
Seed mass on main stem	-0.120	0.687	0.157	0.193	0.337	0.162
Seed mass on lateral branches	0.760	-0.436	-0.126	-0.041	-0.256	-0.125
Seed yield per plant	0.625	0.302	0.043	0.202	0.107	-0.185
1000-seed mass	-0.093	-0.61	-0.574	-0.047	0.127	-0.165

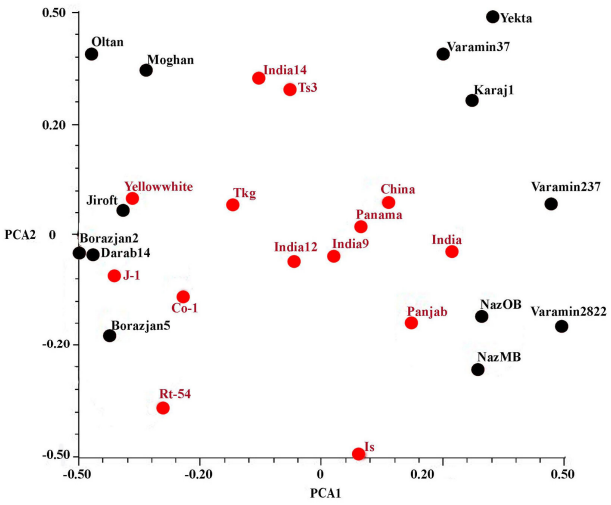

Fig 5. Results of the principal coordinate analysis (PCA) for 27 studied sesame genotypes based on 15 RAPD primers. Black symbols and font correspond to native genotypes and red symbols and font to exotic genotypes (Table 1 for genotypes and Fig. 1 for the cultivation sites of native genotypes).

approximately 40 ng template DNA, 25 pmol of a single decamer primer (Operon Technologies, Alameda, USA), 3 mM $MgCl_2$, 1x reaction buffer (50 mM Tris-HCl, pH 8.0, 100 mM KCl, 0.1 mM EDTA, 1 mM DTT, 50% glycerol and 1% Triton X-100), 0.2 mM dNTP, 1.2 U Taq polymerase (Bio-Rad, Hercules, CA, USA) and distilled water. The PCR program of the thermocycler (iCycler, Bio-Rad, Hercules, CA, USA) was started by a denaturation step of 4 min at 95 °C, followed by 35 cycles of 1 min at 94 °C, 1 min at 36 °C for annealing and 1.5 min at 72 °C for the extension step. After the completion of the cycles, the reaction mixtures were hold at 72 °C for 7 min and then at 4 °C. Amplified products were separated by electrophoresis in a 1.4 % agarose gel in standard Tris/Borate/EDTA buffer (TBE, pH = 8.3), stained with ethidium bromide and photographed under UV light in a gel documentation system (Ultraviolet Products, NY, USA). An 1 kb DNA ladder (Fermentas, HD, Germany) was used as molecular weight standard. Each PCR reaction was repeated

Table 6. Comparison of the degree of genetic variability of sesame accessions observed in different studies

Region	Number of genotypes	Genetic similarity	Clustering method	Molecular markers used (number of markers used)[1]	Reference
Iran	13	0.39 - 0.92	UPGMA	RAPD (15)	This study
Exotic	14	0.4 - 0.81	UPGMA	RAPD (15)	This study
China	404	0.45 - 0.98	UPGMA	SRAP (11), SSR (3)	(Zhang et al., 2010)
India	20	0.78 - 0.95	UPGMA	RAPD (30)	(Kumar and Sharma, 2009)
India	58 (36 Indian, 22 exotic)	0.19 - 0.89	UPGMA	RAPD (16)	(Bhat et al., 1999)
Japan	96	0.21 - 0.93	UPGMA	AFLP(21)	(Ali et al., 2007)
Korea	75	0.84 – 100	UPGMA	ISSR (14)	(Kim et al., 2002)
Sudan	10	0.56 - 0.85	UPGMA	RAPD (10)	(Abdellatef et al., 2008)
Venezuela	20	0.31- 0.78	UPGMA	AFLP (8)	(Laurentin and Karlovsky, 2007)
Venezuela	9	0.15 - 0.53	UPGMA	RAPD (12)	(Salazar et al., 2006)
Venezuela	32	0.38 - 0.85	UPGMA	AFLP (8)	(Laurentin and Karlovsky, 2006)
Vietnam, Cambodia	22	0.57 – 0.97	Neighbour joining	RAPD (10)	(Pham et al., 2009)

[1]AFLP – amplified fragment length polymorphism; ISSR – inter simple sequence repeat; RAPD - random amplified polymorphic DNA; SRAP – sequence-related amplified polymorphism; SSR – simple sequence repeat

at least twice and only reproducible bands were scored. To avoid common problems with RAPD markers (Parani et al., 1997), we have followed rigorous reproducible protocol (Williams et al., 1990). Thirty five decamer primers were used for pre-screening. Bands which were clearly visible in at least one genotype were scored for presence (1) or absence (0) of the band and entered into a data matrix. Out of the 35 primers, 15 primers displayed polymorphism among the genotypes (Table 2) and were used in this study. Altogether, 171 bands were obtained and of these, 111 bands were polymorphic (Fig. 2 and Table 2).

Statistical analysis of morpho-physiological traits

Analyses of variance, correlation, factor and cluster analyses were used to study the statistical relationships among the data and determine the statistical similarity among genotypes due to phenotypic traits. Mean trait values for each variety observed in each block were used as independent replicates. Analysis of variance tested for the effects of plant genotype on phenotypic traits. Correlation analysis evaluated the coordinated variations between the traits measured under the same conditions. For quantitative traits, Pearson pairwise correlation coefficients were utilized, and for qualitative traits (rankings) and for correlations of qualitative traits with quantitative traits, Spearman rank correlation coefficients were calculated. Mean values recorded for each trait (Table 3) were used in the factor analysis (Souza and Sorrells, 1991) to determine the most informative and promising traits best characterizing the overall patterns of variation in plant phenotype. Factors with eigenvalues > 1.0 and with added variance of more than 5% were considered to be relevant. A cluster analysis for morpho-physiological traits was further performed using SPSS version 16 (Norusis, Munich, Germany) based on Ward's method, and the Euclidean distances between the genotypes were calculated after the data standardization. Standardization of the data is essential to reduce the effect of the scale differences among different variables.

Analysis of genetic data

For each primer used, the number of total bands (n_T), polymorphic bands (n_P) and polymorphism percentage (n_P / n_T ×100) were calculated (Table 2). As the measure of genetic distance, Jaccard's coefficient of similarity was employed (Sneath and Sokal, 1963), and calculated for 111 RAPD polymorphic bands. Cluster analysis of RAPD markers for 27 genotypes was performed using NTSYS Software, Version 2.2 (Rohlf, 2005). A dendrogram was constructed based on Jaccard's similarity data applying the unweighted pair group method with arithmetic average (UPGMA). Mantel test was performed by NTSYS Software to evaluate the association between classifications based on 21 quantitative morpho-physiological traits and RAPD data.

Conclusions

This study demonstrates that ecological and geographical factors have shaped the Iranian sesame diversity in complex manner. While there were no broad relationships between genetic diversity and accession origin, there was evidence of closer relatedness of some Iranian genotypes than exotic genotypes, but for other native genotypes, gene flow, possibly reflecting human interference, occurred. Thus, we suppose that human activities were the most important factor affecting the current genetic structure of Iranian sesame accessions. Overall, high genetic diversity is found among Iranian sesame accessions in line with a sesame genetic diversity hotspot in Central Asia.

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