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RESEARCH PAPER

Molecular diversity of Omani wheat revealed by microsatellites: I. Tetraploid landraces

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Abstract Results of archaeological studies indicate a millennia-old cultivation history for wheat (*Triticum* spp.) in Oman. However, in spite of numerous collection surveys and efforts for phenotypic characterization of Omani wheat landraces, no attempts have been made using molecular tools to characterize this germplasm. To fill this gap, 29 microsatellite markers revealing 30 loci were used to study the genetic diversity of 38 tetraploid wheat landrace accessions comprising the species *T. dicoccon*, *T. durum and T. aethiopicum*. A total of 219 alleles were detected whereby the number of alleles per locus ranged from 2 to 16 with an average number of 7.1 alleles per locus. The highest number of alleles occurred in the B genome with on average 7.9 alleles per locus as compared to the A genome with 6.5 alleles per locus. Heterogeneity was detected for all microsatellites except for *GWM 312*, *GWM 601* and *GWM 192B* with an average heterogeneity over all primers and lines of 14.4%. Approximately 10% of the accessions contained rare alleles with an average allele frequency <4%. Gene diversity across microsatellite loci ranged from 0.26 to 0.85. The pairwise comparison of genetic similarity ranged from 0.03 to 0.91 with an average of 0.2. Cluster analysis revealed a clear separation of the two species groups *T. dicoccon* versus *T. durum* and *T. aethiopicum*. Within the species clusters regional patterns of subclustering were observed. Overall, this study confirmed the existence of a surprisingly high amount of genetic diversity in Omani wheat landraces as already concluded from previous morphological analyses and showed that SSR markers can be used for landraces' analysis and a more detailed diversity evaluation.

Keywords Genetic diversity · Molecular markers · Oasis agriculture · *Triticum* spp.

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Introduction

Wheat (*Triticum* spp.) is the world's most important crop based on cultivation area and the second most important after maize (*Zea mays* L.) in total production (FAO 1999). In Oman, where it is traditionally cultivated in remote mountain oases and used for human consumption and animal

feed, wheat has a long cultivation history as indicated by numerous archaeological studies conducted on the Arabian Peninsula. The carbonized rachises and seeds found at archaeological sites date back to 3,500 or even 5,000 BC (Willcox and Tengberg 1995; Potts 1993). These archaeological studies provide evidence that wheat was first introduced through trade from ancient Mesopotamia (Willcox and Tengberg 1995). Subsequently, the introduced germplasm experienced evolutionary modifications resulting from natural selection and adaptation to the harsh desert environment prevailing in the region (Zohary and Hopf 1993).

In the past most assessments of genetic diversity of germplasm were based on morphological traits or isozyme analysis. However, the power of molecular markers as tools to evaluate the genetic diversity of germplasm is increasingly recognized (Szabó and Hammer 1995; Melchinger et al. 1991). Such markers have been used to trace the geographic origins of accessions by comparing genetic fingerprints of diverse material (Wei et al. 2003; Salamini et al. 2002; Baek et al. 2003) and to classify germplasm resources (Zhang et al. 2004; Alamerew et al. 2004). Microsatellites are, compared to other marker types, abundant, ubiquitous in presence, possess a high polymorphism information content (PIC) and are often multiallelic (Röder et al. 1995; Gupta et al. 1996). A limited number of microsatellite markers is often sufficient to detect differences even in very closely related wheat genotypes (Plaschke et al. 1995). Furthermore, a large number of wheat microsatellite markers have been developed which are widely used in genomic mapping, population and evolutionary studies, as well as for fingerprinting and pedigree analyses (Röder et al. 1998, 2004).

Crop diversity studies using molecular markers have been conducted in barley (*Hordeum vulgare* L.; Macaulay et al. 2001; Matus and Hyes 2002; Koebner et al. 2003), rice (*Oryza sativa* L.; Ishii et al. 2001; Temnykh et al. 2001), maize (*Zea mays* L.; Mumm and Dudley 1994; Smith et al. 1997; Lu and Bernardo 2001), in winter triticale (*Triticosecale* Wittm.; Tams et al. 2004) and in wheat (*Triticum* spp.; Donini et al. 2000; Prasad et al. 2000; Russell et al. 2000; Röder et al. 2002; Huang et al. 2002; Eujayl et al. 2002; Soleimani et al. 2002). Microsatellites have a high potential for genome analyses in self-pollinating crops because of their specific properties and their high degree of polymorphism (Plaschke et al. 1995; Röder et al. 1995). Genetic variation in the studied crop can be detected by primers flanking the microsatellite locus in the selected DNA sequences (Johansson et al. 1992; Rongwen et al. 1995).

Given its overall limited importance for small-scale farmers' income and the remoteness of most cultivation sites, no attempt has been made so far to characterize Omani wheat by molecular means. This study was therefore conducted to evaluate the genetic diversity of tetraploid wheat landraces collected from Oman, using microsatellites (SSR) as molecular markers.

Materials and methods

Plant material

A total of 38 tetraploid wheat landraces were collected from different cultivation areas of Oman (Fig. 1; Table 1). Several seeds of representative spikes of all accessions were sown for further study at the greenhouse of the Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben, Germany.

DNA extraction, polymerase chain reaction and amplification

Total genomic DNA was extracted from pooled leaves of six seedlings derived from six seeds of any one spike. The extraction was performed according to Plaschke et al. (1995). Amplifications by polymerase chain reaction (PCR) were performed as described by Röder et al. (1998). The PCR reaction substrate contained 50–100 ng template DNA, 250 nM cy5-labelled forward primer, 250 nM unlabelled reverse primer, 0.2 mM dNTPs, PCR buffer with a final concentration of 1.5 mM $MgCl_2$ and 1 U *Taq* DNA polymerase in a total volume of 25 µl. Fragment detection was performed by an Automated Laser Fluorescence (ALFexpress) sequencer (Amersham Biosciences) and fragment

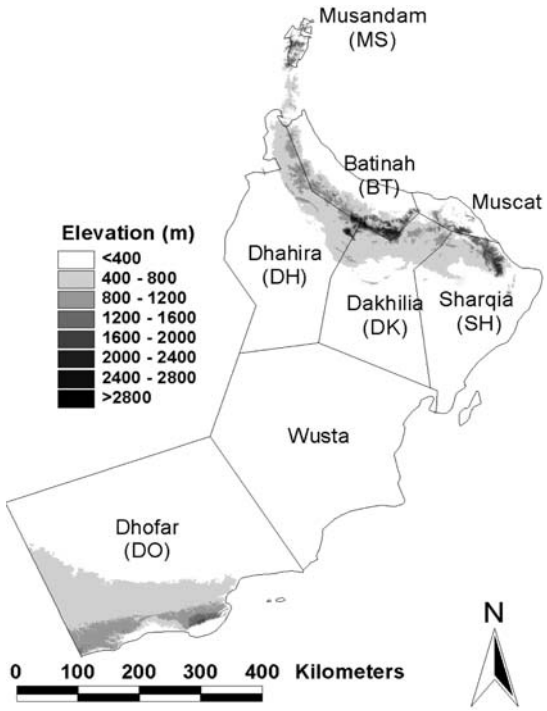

Fig. 1 Map of Oman indicating the districts where the tetraploid wheat landraces were collected

sizes were calculated using the computer programme Fragment Analyser 1.02 (Amersham Biosciences – GE Healthcare, USA) by comparison with internal size standards. In the case of weak or lacking fragment products, PCR amplifications were repeated to exclude failed PCR reaction as the cause of a null allele.

Microsatellite loci

Twenty-eight Gatersleben Wheat Microsatellites (GWM) and one microsatellite from a pseudogliadine gene, *Taglgap*, representing approximately two markers for each chromosomes of the A and B genomes were used in the study (Table 2). These microsatellite primers were described by Röder et al. (1998) and the primer *Taglgap* by Devos et al. (1995). Microsatellite loci *GWM337-1DS, GWM157-2DL, GWM3-3DS, GWM190-5DS, GWM325-6DS* and *GWM4377DL* that represent the D genome were used to check for the presence of mixtures of hexaploid accessions in the Omani tetraploid wheat landraces. These primers failed to amplify fragments from all lines except for the hexaploid standards.

Data analysis

The presence and absence of specific microsatellite alleles was scored in a binary data matrix. The wheat varieties 'Chinese Spring' and 'Aztec' were used as controls to standardize different gel runs. The gene diversity also called polymorphism information content (PIC) was computed according to Nei (1973) as

$$\mathrm{PIC} = 1 - \sum P_{ij}^2$$

where P_{ij} is the allele frequency of the jth allele for the ith marker summed over numbers of alleles. Anderson et al. (1993) suggested that gene diversity is the same as the polymorphism information content (PIC). Genetic similarity (GS) according to Nei and Li (1979) was calculated as

$$\mathrm{GS} = 2N_{ij}/(N_i + N_j)$$

Where N_{ij} is the number of fragments common to lines i and j, and $(N_i + N_j)$ is the total number of fragments in both lines.

All fragments were used to generate a genetic similarity matrix with the software NTSYS (Numerical Taxonomy and Multivariate Analysis System, vers. 2.1 for PC (Rohlf 2002). The relationships among accessions were analyzed using the unweighted pair-group method (UPGMA) and principle component analysis (PCA; Sneath and Sokal 1973). The ordination analysis was carried out using the similarity coefficient introduced by Dice (1945).

Results

Analysis of allelic diversity by microsatellites

A total of 219 alleles was detected with the 29 microsatellites markers for 30 loci used to evaluate and characterize the genetic diversity of the 38 tetraploid wheat landraces. The number of alleles per locus ranged from two for *GWM752*,

Table 1 List of tetraploid wheat accessions collected from different districts of Oman with their catalogue number (OMTRI) and botanical name

OMTRI	Collection district	Botanical name
192	Batinah (BT)	*T. dicoccon* Schrank
193		*T. dicoccon* Schrank
195		*T. aethiopicum* Jakubz.
196		*T. durum* Desf. var. *africanum* Koern.
197		*T. durum* Desf. var. *africanum* Koern.
198		*T. durum* Desf. var. *affine* Koern.
199		*T. aethiopicum* Jakubz. var. *bialbum* (Vav.) A. Filat.
200		*T. aethiopicum* Jakubz. var. *comitans* (Vav.) A. Filat.
201		*T. aethiopicum* Jakubz. var. *comitans* (Vav.) A. Filat.
202		v.n.[a]
203		*T. aethiopicum* Jakubz. var. *hajirense* (nom. nud.)
204		*T. durum* Desf. var. *africanum* Koern.
205		*T. aethiopicum* Jakubz. var. *densifulvum* (Vav.) Dorof. et A. Filat.
206		*T. durum* Desf. var. *africanum* Koern.
207		*T. durum* Desf. var. *melanopus* (Alef.) Koern.
208		*T. durum* Desf. var. *mahsinense* (nom. nud.)
209		*T. aethiopicum* Jakubz. var. *comitans* (Vav.) A. Filat.
210		*T. aethiopicum* Jakubz. var. *syrovatskyi* (Vav.) A. Filat.
211		*v.n.*
212		*T. aethiopicum* Jakubz. var. *comitans* (Vav.) A. Filat.
213		*T. aethiopicum* Jakubz. var. *pseudorarum* (Vav.) A. Filat.
218	Dhahira (DH)	*T. aethiopicum* Jakubz. var. *comitans* (Vav.) A. Filat.
219		*T. aethiopicum* Jakubz. var. *syrovatskyi* A. Filat.
220		*v.n.*
221		*v.n.*
25	Dakhilia (DK)	*T. dicoccon* Schrank ssp. *asiaticum* Vav. var. *haussknechtianum* A. Schulz
23		*T. dicoccon* Schrank ssp. *asiaticum* var. *haussknechtianum* A. Schulz
19A		*T. aethiopicum* Jakubz. var. *tchertchericum* (Vav.) A. Filat.
19B		*T. aethiopicum* Jakubz. var. *tchertchericum* (Vav.) A. Filat.
194	Dhofar (DO)	*T. dicoccon* Schrank
222	Musandam	*T. aethiopicum* Jakubz. var. *pilosinigrum* (Vav.) A. Filat.
223	(MS)	*T. aethiopicum* Jakubz. var. *tchertchericum* (Vav.) A. Filat.
24	Sharqia (SH)	*T. dicoccon* Schrank ssp. *asiaticum* Vav. var. *haussknechtianum* A. Schulz
29		*T. dicoccon* Schrank ssp. *asiaticum* Vav. var. *aeruginosum* Flaksb.
214		*T. aethiopicum* Jakubz. var. *syrovatskyi* A. Filat.
215		v.n.
216		*T. aethiopicum* Jakubz. var. *syrovatskyi* A. Filat.
217		*T. aethiopicum* Jakubz. var. *syrovatskyi* A. Filat.

[a] v.n. = unidentified (potentially new) botanical variety

GWM619, *GWM192a*, *GWM*415 and *GWM*680 to 16 for *GWM*186 with an average number of 7.3 alleles per locus (Table 2). All microsatellites used in this study yielded polymorphic fragments for the evaluated accessions. At the genome level, a larger number of alleles per locus occurred in the B genome (7.88 alleles per locus) than in the A genome (6.54 alleles per locus).

Heterogeneity represented by more than one amplification product for one microsatellite locus was detected for all microsatellites except for *GWM312*, *GWM601* and *GWM192B* (Table 2). The average of the heterogeneity estimated over all 30 primers was 14.4% and represents the heterogeneity within durum landraces investigated as bulked DNA from six plants in the analysis. A

Table 2 Thirty wheat microsatellite loci (GWM) of known chromosomal location used to evaluate allele variation, product size (bp), number of alleles (rare alleles), gene diversity (PIC) and percentage of heterogeneity per locus in tetraploid wheat landraces from Oman

GWM Chromosomal location	Range of allele size (bp)	No. of alleles (rare alleles)	PIC	Heterogeneity per locus (%)
Xgwm 357 – 1AL	118–126	6 (1)	0.643	2.63
Xgwm 752 – 1AS	121–123	2 (1)	0.411	5.26
Xgwm 268 – 1BL	Null, 177–24	11 (4)	0.851	5.26
Xgwm 18 – 1BS	177–189	7	0.769	15.79
Taglap – 1BS	232–271	8 (2)	0.742	15.79
Xgwm 148 – 2BL	141–167	10 (2)	0.575	34.21
Xgwm 312- 2AL	204–250	8 (2)	0.753	0.00
Xgwm 95 – 2AS	108–122	6	0.722	5.26
Xgwm 619 – 2BL	143–155	2	0.260	18.42
Xgwm 155 – 3AL	129–149	7	0.757	23.68
Xgwm 720 – 3AS	130–168	12 (5)	0.733	21.05
Xgwm 655 – 3BL	Null, 160–174	6 (2)	0.585	7.89
Xgwm 389 – 3BS	102–156	12 (2)	0.771	39.47
Xgwm 160 – 4AL	176–1186	5 (1)	0.563	10.53
Xgwm 192 – 4AL	128–134	2	0.303	7.89
Xgwm 601 – 4AS	Null, 150–160	8 (2)	0.819	0.00
Xgwm 192 – 4BL	Null, 197–209	7 (1)	0.801	0.00
Xgwm 513 – 4BL	139–149	6	0.535	36.84
Xgwm 898 – 4BS	95–119	7 (2)	0.318	31.58
Xgwm 186 – 5AL	Null, 94–152	16 (2)	0.744	76.32
Xgwm 415 – 5AS	126–132	2	0.000	5.26
Xgwm 408 – 5BL	147–193	6	0.658	15.79
Xgwm 540 – 5BS	126–130	3	0.467	10.53
Xgwm 427 – 6AS	186–212	6 (1)	0.609	23.68
Xgwm 219 – 6BL	Null, 120–184	14 (8)	0.983	7.89
Xgwm 680 – 6BS	126–132	2 (4)	0.767	21.05
Xgwm 631 – 7AS	190–202	5	0.527	13.16
Xgwm 297 – 7B(C)	152–178	10 (5)	0.823	21.05
Xgwm 577 – 7BL	Null, 126–210	13 (2)	0.959	28.95
Xgwm 333 -7BL	148–168	10	0.813	5.26
Minimal		**2**	**0.00**	
Maximal		**16**	**0.96**	
Total		**219 (51)**	**19.26**	
Average		**7.3 (1.7)**	**0.64**	

particularly large amount of heterogeneity was present in the accessions *T. durum* var. *affine* (OMTRI 198) and *T. aethiopicum* var. *bialbum* (OMTRI199). Both were collected in the Khabura region in the Centre of the Batinah district.

Rare alleles were detected in most of the microsatellite loci and occurred once per locus. In total, 51 different rare alleles were detected ranging from one rare allele per locus (*GWM357, GWM192b* and *GWM427*) to five alleles per locus (*GWM577* and *GWM720*) with an average frequency of rare alleles of 4% (Table 2).

Some primers *GWM268, GWM655, GWM601, GWM192B, GWM898, GWM219* and *GWM577* were unable to produce fragments in certain accessions (Table 2). Before considering them as null alleles, the experiments were repeated.

The polymorphism information content (PIC) across the 30 microsatellite loci ranged from monomorphic for *GWM415* to 0.85 for *GWM268* (Table 2). The B genome was with a PIC value of 0.69 more polymorphic than genome A (0.58). The rank correlation over the 30 microsatellites loci, calculated to evaluate the relationship between the gene diversity and number of alleles, was $r = 0.71$ (Fig. 2). This indicated a significant correlation between gene diversity and numbers of alleles in all accessions.

Cluster analysis

The GS ranged from 0.09 for OMTRI 216 (*T. aethiopicum* var. *syrovatskyi*) and OMTRI 217 (*T. aethiopicum* var. *syrovatskyi*) and 0.97 for

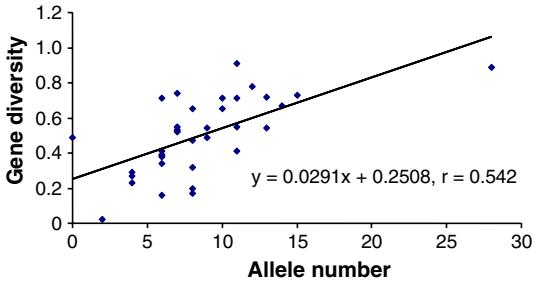

Fig. 2 Correlation between number of alleles and gene diversity of 38 Omani cultivated tetraploid wheat landraces

OMTRI 192 (*T. dicoccon*) and OMTRI 201 (*T. aethiopicum* var. *comitans*).

Cluster analysis allowed to discriminate two major groups. The first cluster consisted only of emmer wheat *(T. dicoccon)*, while the second cluster comprised the other botanical varieties (Fig. 3). The second cluster contained several subclusters which partly represented the geographical distribution of the collection sites. One subcluster contained accessions collected in the districts of Dakhilia (*OMTRI 19A, 19B*), Dhahira (OMTRI 220 and 221) and Sharqia (OMTRI 215, 216 and 217). Another subcluster combined two accessions from the Dhahira district (OMTRI 218 and 219) with two accessions collected in the Musandam district (OMTRI 222 and 223) and one accession from the Batinah district (OMTRI 213). The other subclusters were represented by accessions from the Batinah district, which comprise the majority of the collected accessions. Here also subclustering was observed, for example for accessions collected at Sohar (OMTRI 208-213) or accessions collected at Khabura (OMTRI 196-201).

Similar to the cluster analysis principal coordinate analysis (PCA) separated the accessions into two groups with *T. dicoccon* versus *T. durum and T. aethiopicum*. This confirmed the results of the cluster analysis whereby the first three principle components accounted for 54.1% of the total variation in the microsatellite markers (Fig. 4).

Discussion

A total of 219 alleles were generated from 38 cultivated tetraploid wheat landraces using 29 microsatellite markers. The average number of alleles was 7.3 and genome B was more polymorphic than A. These results were similar to previous studies in wheat (Figliuolo and Perrino 2004) who reported that 15 markers produced 63 bands with an average of 7.7 alleles. Moreover, Teklu et al.

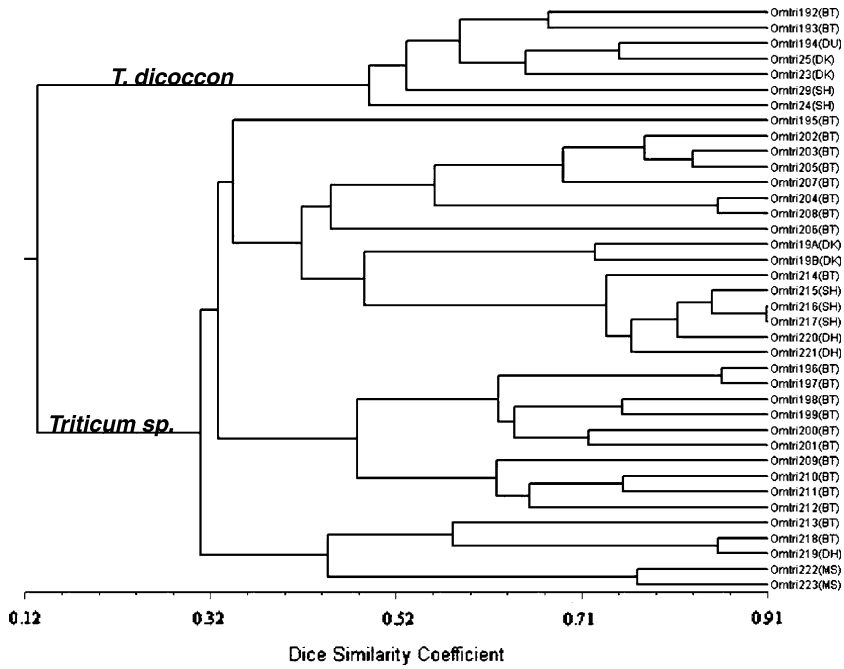

Fig. 3 Dendrogram of 38 landrace accessions from Oman based on the UPGMA clustering of data derived from 30 microsatellite loci

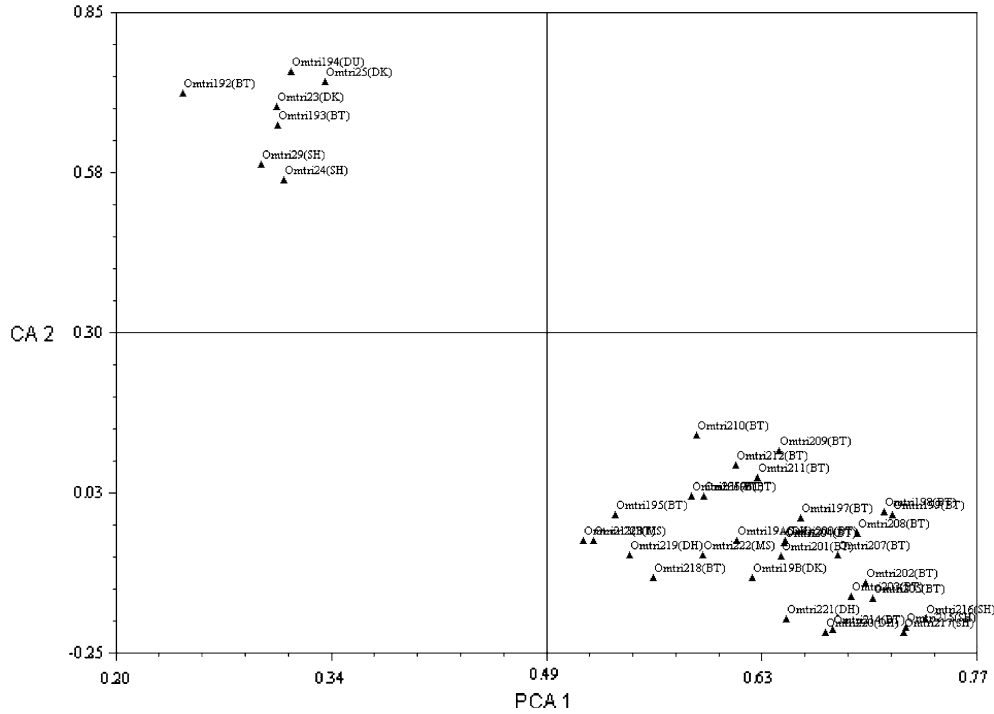

Fig. 4 Scattergram of 38 landrace accessions from Oman based on the principal coordinate analysis (PCA) of 30 microsatellite loci

(2006) reported a higher number of alleles per locus for *T. durum* than for *T. turgidum* and *T. dicoccon*. Their 29 SSR markers revealed 320, 202 and 271 alleles in *T. durum*, *T. dicoccon* and *T. turgidum* landraces, respectively. The average number of alleles per locus was 11.0 in *T. durum*, 7.0 in *T. dicoccon* and 9.3 in *T. turgidum*. On the other hand Eujayl et al. (2001) found an average of 5.5 alleles per locus with 64 genotypes. Bertin et al. (2001) detected an average number of 5.2 alleles per locus in spelt wheat (*T. spelta* L.) and Ben Amer et al. (2001) used 24 wheat microsatellites to estimate 15 Libyan wheat genotypes thereby detecting 116 alleles with an average of 4.5 alleles per locus. The occurrence of null alleles in the material of our study was also observed in materials analysed by Röder et al. (2002), Ben Amer et al. (2001); Alamerew et al. (2004) and Teklu et al. (2006). In general, the present study confirmed the presence of a high genetic diversity in Omani wheat landraces as it was suggested by previous studies of morphological diversity (Al-Maskri et al. 2003, Hammer et al. 2004).

The average gene diversity obtained in the present investigation was 0.64. These results confirm earlier studies in tetraploid wheat species from Ethiopia using microsatellite analysis where the average gene diversity across the 29 microsatellite loci was 0.68 for *T.* durum, 0.616 for *T. dicoccon* and 0.688 for *T. turgidum* wheat (Teklu et al. 2006). The results were also similar to those reported by Khlestkina et al. (2004) who showed an averaged gene diversity of 0.70 in 54 Siberian wheats. Anderson et al. (1993) found a PIC of 0.71 in spring wheats. In the study of 105 Argentinean wheat varieties Manifesto et al. (2001) found an average gene diversity of 0.72 compared to an average PIC value of 0.674 in European wheat varieties reported by Röder et al. (2002). Huang et al. (2002) characterized 998 wheat accessions at the Gatersleben geneb bank and reported a gene diversity of 0.77. All of these values were high compared to a gene diversity of 0.24 for winter wheat reported by Bohn et al. (1999).

The rather high genetic diversity in the Omani durum landraces is most likely the result of its

long cultivation history in relatively isolated mountain oasis systems which enhanced the effects of natural and artificial selection on germplasm diversity.

Gene diversity per locus showed a linear correlation with the number of alleles. These results confirm previous findings by Huang et al. (2002) and Roussel et al. (2004). Prasad et al. (2000), in contrast, reported that the PIC value was not correlated with the number of alleles. The levels of heterozygosity found in our germplasm were similarly high than those reported by Alamerew et al. (2004) and Röder et al. (2002) for Ethiopian and European wheats but much higher than those found by Kudryavtsev et al. (2004) in Russian *T. durum* varieties.

The cluster analysis allowed to separate the Omani landraces into two major groups, emmer wheat and other *Triticum* spp. Moreover, in the dendrogramme, accessions belonging to *Triticum aethiopicum* were mostly grouped together in clusters indicating the uniqueness of this group. Khlestkina et al. (2004) and Huang et al. (2002) reported that not all accessions originating from the same geographic region clustered in the same group. These findings are in agreement with those of the current study. In contrast, Ben Amer et al. (2001) showed that clustering of accessions can be strongly related to geographic origin and ploidy level of the germplasm.

Conclusions

The molecular analyses of tetraploid wheats reported in this study confirm earlier morphological work showing a surprisingly high diversity in traditional landraces from Oman. This diversity likely reflects the effects of the germplasm's millennia-old selection history and of the many agro-environmental niche environments in remote mountain oases. The study also shows the power of microsatellites in discriminating landraces and revealing heterogeneity from individual accessions. Finally, it calls for continued efforts to further study and preserve Omani wheats in situ and ex situ through proper policy measures.

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