

Molecular diversity of Omani wheat revealed by microsatellites: II. Hexaploid landraces

S. Al Khanjari · K. Hammer · A. Buerkert ·
M. S. Röder

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Abstract For millennia, wheat (*Triticum* spp.) has been grown in traditional aflaj-irrigation systems of remote mountain oases in Oman. However, little is known about the diversity of the ancient landraces used. Given recent reports about the occurrence of novel germplasm in such material, the objective of this study was to evaluate the genetic diversity of hexaploid wheat (*Triticum aestivum* L.) landraces in relation to their geographic origin using microsatellites. The collection covered most of the cultivation areas in northern Oman where wheat landraces are growing. Total genomic DNA was extracted from six pooled plants representing each accession. A total of 161 wheat accessions were assayed using 35 microsatellite loci in which a total of 305 polymorphic bands were recorded for the 35 microsatellites. The polymorphic information content (PIC) across the 35 microsatellite loci ranged

from 0.02 to 0.89 with an average of 0.50. A heterozygosity percentage value of 9.09 was determined and the highest level recorded for accessions from the Batinah district. Rare alleles averaged 1.85 with the highest value being from the Dakhilia district. The results indicated a significant correlation between gene diversity and number of alleles across districts. The correlation coefficient between these two variables over the 35 loci was 0.657, whereby correlation coefficients of 0.718, 0.706, 0.657 and 0.651, respectively, were found for the Batinah, Dhahira, Dakhilia and Sharqia materials. Genetic distances indicated that all landraces were closely related. The cluster analysis discriminated most of the landraces accessions. However, it failed to achieve region-specific groupings of landraces. The present study demonstrated the presence of high diversity in Omani landraces and also indicated the effectiveness of microsatellites to describe it.

S. Al Khanjari · K. Hammer · A. Buerkert (✉)
Institute of Crop Science, University of Kassel,
D-37213 Witzenhausen, Germany
e-mail: buerkert@uni-kassel.de

S. Al Khanjari
College of Agriculture and Marine Sciences, Sultan
Qaboos University, Al Khod, Oman

M. S. Röder
Institute of Plant Genetics and Crop Plant Research
(IPK), Corrensstrasse 3,
D-06466 Gatersleben, Germany

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Introduction

Only recently Omani wheat landraces, grown in remote mountain oases, have attracted the attention of scientists despite the millenia-old

cultivation history of *Triticum* spp. on the Arabian Peninsula (Schwartz 1939; Guarino 1990; Potts 1993; Zohary and Hopf 1993; Willcox and Tengberg 1995). First morphological studies showed a surprisingly large phenotypic variation and the presence of at least six so far undescribed hexaploid (*T. aestivum* L.) and three tetraploid (*T. durum* Desf., *T. aethiopicum* Jakubc.) botanical wheat varieties (Al-Maskri et al. 2003; Hammer et al. 2004).

The diversity of germplasm has traditionally been described using morphological and agronomical traits (Vavilov 1964; Chapman 1985). However, molecular markers such as microsatellites (SSRs) have been found to be complementary to morphological, pedigree, heterosis and biochemical data (Tolbert et al. 1979; Doebley 1989; Melchinger et al. 1991). Microsatellites have a high potential use for the genetic analysis of self-pollinating crops because of their high degree of polymorphism and they are codominantly inherited (Akkaya et al. 1992; Plaschke et al. 1995; Röder et al. 1995, 2004). Primers flanking the microsatellite locus in the selected DNA sequences even allow to detect multiallelic variation (Johansson et al. 1992; Rongwen et al. 1995). Previously microsatellites have been successfully used in diversity studies of wheat and barley (Koebner et al. 2003; Prasad et al. 2000; Russell et al. 2000; Eujayl et al. 2002; Soleimani et al. 2002; Melchinger et al. 1994). Also, extensive information about their use is available for rice (*Oryza sativa* L.; Ishii and McCouch 2001; Temnykh et al. 2001) and maize (*Zea mays* L.; Mumm and Dudley 1994; Smith et al. 1997; Lu and Bernardo 2001).

Lately, microsatellites have been used to trace the geographic origin of accessions by fingerprinting diverse germplasm from different regions and may thus also help to trace the pre-historic spread of germplasm (Baek et al. 2003; Huang et al. 2002; Li et al. 2002; Röder et al. 2002; Salamini et al. 2002; Zhang et al. 2006).

In view of the above the purpose of this study was to assess the value of molecular markers in unraveling the genetic structure of hexaploid wheat landraces from Oman.

Materials and methods

Plant material

A survey was conducted in the two spring seasons of 2002–2003 across the wheat growing districts of Oman which covered about 80% of the total cultivated area in the country (Fig. 1). At each location, a few randomly chosen farmers were interviewed to identify individuals who still grew landraces of wheat. All of the indicated fields, mostly in remote mountain oases, were visited, whenever physically possible and representative germplasm for each of the 161 hexaploid wheat accessions were collected. Seeds from all accessions were planted in the green house at the Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben, Germany (Table 1).

DNA extraction, polymerase chain reaction and amplification

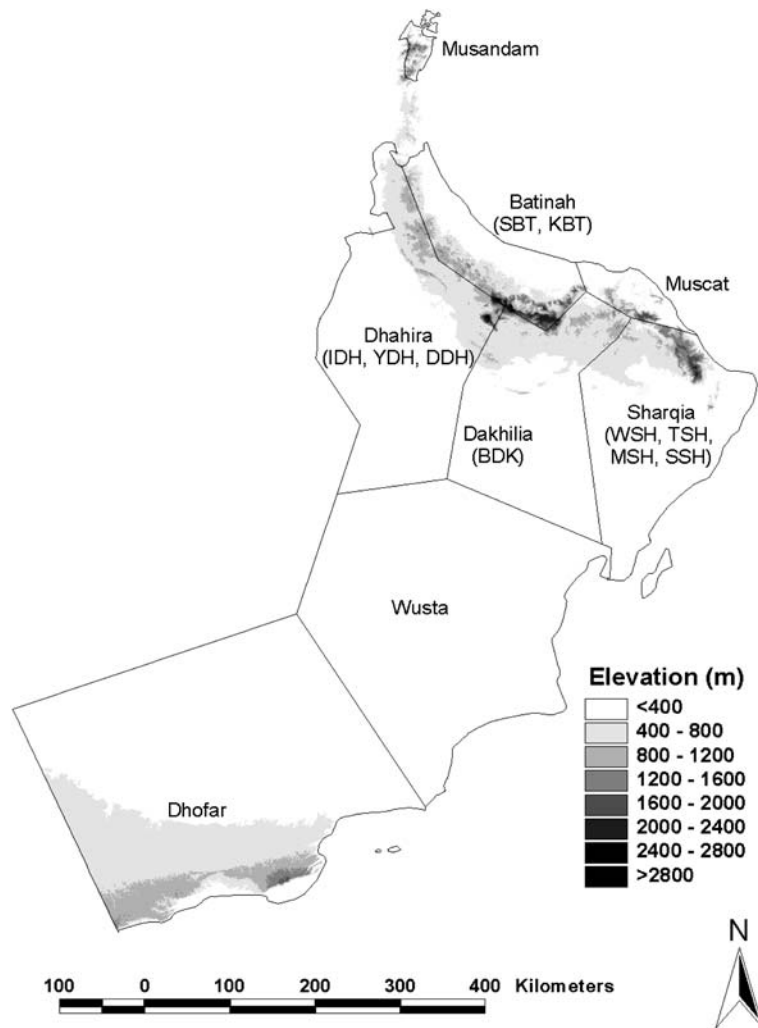
Total genomic DNA was extracted from pooled leaves of six 3-week-old plants grown from representative seeds of any accession. To this end the young seedling leaves of each accession were harvested and frozen in liquid nitrogen. Subsequently, approximately 3–5 g of leaf material were ground into a fine powder and poured into 50 ml propylene tubes.

The extraction was performed according to Fulton et al. (2000) with an extraction buffer described in Plaschke et al. (1995). Polymerase chain reaction amplifications were performed as described by Röder et al. (1998). All further steps were identical to those mentioned by Al Khanjari et al. (2006).

Microsatellite markers (SSR)

A total of 35 SSR primers were produced from Gatersleben wheat microsatellites (GWM) and one of them from a pseudogliadine gene, Taggap. The markers were selected based on their uniformity of distribution in the genome level. Approximately three markers for each chromosome of the A, B and D genomes were used in the study. The microsatellite primers used (Table 2) were

Fig. 1 Map of Oman indicating the four districts Dhahira (*YDH* Yanqul, *DDH* Dank, *IDH* Ibri), Batinah (*SBT* Sohar, *KBT* Khabura), Dakhilia (*BDK* Bahla) and Sharqia (*SSH* Sur, *WSH* Al Raky, *TSH* Taen, *MSH* Maqta) where the hexaploid wheat landraces were collected



previously described by Röder et al. (1998) and for the primer Taglgap by Devos et al. (1995).

Data analysis

The presence (1) and absence (0) of specific microsatellite alleles was scored in a binary data matrix. ‘Chinese Spring’ and ‘Aztec’ were used as controls to standardize different gel runs. The gene diversity also called polymorphic information content (PIC) was computed according to Nei (1973) as:

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

where P_{ij} is the allele frequency of the j th allele for the i th marker summed over the number of

alleles. Anderson et al. (1993) suggested that gene diversity is the same as the PIC.

Genetic similarity (GS; Dice 1945) was calculated as:

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

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

Genetic distance (GD) among group pairs was calculated following (Nei and Li 1979).

$$(\text{GD}_{xy}) = 1 - (2N_{xy}/N_x + N_y)$$

To calculate allele frequency (A_{xy}) from one group of variation to another in each locus the formula of Khlestkina et al. (2004) was used:

Table 1 OMTRI (Oman *Triticum*) accession numbers of hexaploid wheat landraces from Oman used for molecular genetic analysis in this diversity study

District	Region	OMTRI	Total
Batinah	Sohar (SBT)	125, 159, 160, 161, 162, 163, 164, 165, 166, 167, 168, 169, 170, 171, 172, 173, 174, 175, 176, 177, 178, 179	22
	Khabura (KBT)	180, 181, 182, 183, 184, 185, 186, 187, 188, 189, 190, 191	12
Dhahira	Ibri (IDH)	51, 54, 55, 56, 57, 58, 59, 60, 61, 62, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 107, 108, 109, 110, 111, 112, 113, 114, 115, 116, 117	31
	Dank (DDH)	50, 63, 64, 65, 66	5
	Yanqul (YDH)	52, 53, 67, 68, 69, 70, 71, 72, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105, 106, 118, 119, 120, 121, 122	37
Dakhilia	Bahla (BDK)	30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49	20
Sharqia	Sur (SSH)	123, 124, 157, 158	4
	Taeen (TSH)	139, 140, 141, 142, 143, 144, 156	7
	Al Raky (WSH)	126, 127, 128, 129, 130, 131, 132, 134, 135, 136, 137, 138, 155	13
	Maqta (TMSH)	145, 146, 147, 148, 149, 150, 151, 152, 153, 154	10
Total			161

$$\text{Allele frequency variation} = \frac{\sum |P_{xi} - P_{yi}|}{N_{xy}} \times 100\%$$

where P_{xi} and P_{yi} are the frequencies of the i th allele in regions X and Y , respectively, and N_{xy} is the total number of alleles for the two groups X and Y .

The allelic frequency variation (A_{xy}) was calculated separately for each of the 35 loci and then for all of them as an average.

All fragments were used to generate a GS matrix with the software NTSYS (Numerical Taxonomy and Multivariate Analysis System, vers. 2.1) for PC (Rohlf 2002). The relationships among accessions were analysed using the un-weighted pair-group methods (UPGMA) and principal component analysis (PCA; Sneath and Sokal 1973).

Results

Microsatellites

The 35 wheat microsatellite markers used revealed a total of 305 alleles. Their fragment size ranged from 77 bp in *GWM3* located on chromosome 3DS to 265 bp in *Taglgap* on chromosome

1BS. The average number of alleles/locus was 8.70 and the largest number of alleles (28 alleles) was detected at locus *GWM459*. The lowest number of alleles (2 alleles) was at *GWM261* (Table 2).

District-wise analysis of diversity parameters was based on different numbers of accessions. Averages of allele numbers were different for each district. With 245 the allele number was highest in the Dhahira district followed by Batinah (198), Sharqia (161) and Dakhilia (126). The average allele numbers per district were strongly correlated to the number of investigated accessions ($r = 0.93$).

The number of rare alleles (frequency < 0.02) significantly varied between markers ranging from 0 for *GWM357*, *GWM155*, *GWM655*, *GWM192A* and *GWM192D* to 5 on *GWM540* with total alleles averaging 1.76 (Table 2). The highest number of rare alleles was observed for Batinah (67) followed by Dhahira (57), Dakhilia (38) and Sharqia (36) (Table 3). The eight unique alleles were found at *GWM752*, *GWM18*, *GWM3*, *GWM192B*, *GWM898*, *GWM408*, *GWM44* and *GWM333*.

Heterozygosity was observed for all microsatellite loci but the heterozygosity level varied

Table 2 List of the 35 microsatellite loci of chromosome locations used to evaluate allele variation, range of fragment size, genetic diversity, polymorphism information content (PIC), allele number, rare alleles, heterozygosity (H) and allele variation (AV) of 161 hexaploid wheat landraces from Oman

SSR and chromosomal location	Fragment size range	PIC	Allele no.	Rare alleles	H (%)	AV (%)
<i>XGWM357-1AL</i>	120–126	0.49	4	0	2	1.31
<i>XGWM752-1AS</i>	Null, 120–154	0.71	6	1	8	1.97
<i>XGWM18-1BS</i>	177–193	0.47	8	1	16	2.62
<i>Taglgap-1BS</i>	Null, 212–265	0.49	9	2	6	2.95
<i>XGWM458-1DL</i>	Null, 108–170	0.32	8	2	7	2.62
<i>XGWM337-1DS</i>	110–168	0.41	11	2	15	3.61
<i>XGWM95-2AS</i>	Null, 129–124	0.17	8	3	5	2.62
<i>XGWM619-2BL</i>	143–179	0.54	9	3	32	2.95
<i>XGWM157-2DL</i>	Null, 98–112	0.2	8	2	6	2.62
<i>XGWM261-2DS</i>	Null, 163–175	0.29	4	2	3	1.31
<i>XGWM155-3AL</i>	Null, 129–149	0.53	7	0	27	2.30
<i>XGWM720-3AS</i>	130–182	0.73	15	3	36	4.92
<i>XGWM655-3BL</i>	Null, 158–172	0.65	8	0	12	2.62
<i>XGWM389-3BS</i>	Null, 102–160	0.67	14	3	23	4.59
<i>XGWM3-3DS</i>	Null, 77–85	0.41	6	1	4	1.97
<i>XGWM160-4AL</i>	176–198	0.52	7	2	7	2.30
<i>XGWM192-4AS</i>	128–134	0.02	2	0	1	0.66
<i>XGWM192-4BL</i>	Null, 191–225	0.71	11	1	13	3.61
<i>XGWM513-4BL</i>	143–151	0.39	6	2	16	1.97
<i>XGWM898-4BS</i>	103–115	0.23	4	1	10	1.31
<i>XGWM192-4DL</i>	Null, 134–140	0.27	4	0	1	1.31
<i>XGWM186-5AL</i>	Null, 126–152	0.54	13	3	34	4.26
<i>XGWM415-5AS</i>	120–134	0.91	11	2	10	3.61
<i>XGWM408-5BL</i>	Null, 175–183	0.34	6	1	10	1.97
<i>XGWM540-5BS</i>	114–138	0.65	10	5	34	3.28
<i>XGWM190-5DS</i>	200–214	0.55	7	2	12	2.30
<i>XGWM459-6AS</i>	Null, 162–190	0.89	28	2	26	9.18
<i>XGWM680-6BS</i>	123–147	0.38	6	1	7	1.97
<i>XGWM325-6DS</i>	Null, 122–142	0.74	7	1	24	2.30
<i>XGWM631-7AS</i>	Null, 190–204	0.39	6	2	20	1.97
<i>XGWM297-7B(C)</i>	Null, 150–178	0.71	10	2	15	3.28
<i>XGWM333-7BL</i>	148–166	0.16	6	1	4	1.97
<i>XGWM577-7BL</i>	Null, 126–224	0.72	13	2	10	4.26
<i>XGWM437-7DL</i>	Null, 98–118	0.55	11	3	28	3.61
<i>XGWM 44-7DS</i>	Null, 152–186	0.78	12	1	28	3.93

Table 3 Comparison of gene diversity (polymorphism information content, PIC values) of cultivated bread wheat landraces among the different districts of Oman

	Dhahira	Batinah	Sharqia	Dakhilia	Total
No. of accession	74	34	33	20	161
Allele numbers	245	198	161	126	305
Average no. of alleles per marker	7.00	5.67	5.00	5.57	8.70
No. of rare alleles	57	67	36	38	61
No. of unique alleles	5	1	1	0	8
Heterozygosity %	9.00	10.57	12.57	14.38	9.09
Average PIC value	0.45	0.48	0.42	0.33	0.5

among microsatellite markers. It was highest at locus *GWM186* of chromosome 5A and lowest at *GWM192* of chromosome 4D. The highest percentage of heterozygosity was in Dakhilia district

(14.4%) and the lowest in Sharqia (12.6%, Table 3)

The allelic frequency variation within loci indicated the highest variation for *GWM459* and

the lowest for *GWM192A* with 9.2 and 0.7%, respectively (Table 2).

Analysis of gene diversity

The PIC-value reflecting the gene diversity of the 35 microsatellite loci ranged from 0.02 at locus *GWM 192A* to 0.89 at locus *GWM459* with an average of 0.50 (Table 2). The gene diversity differed between districts (Table 3). The correlation coefficient between gene diversity and numbers of alleles over the 35 microsatellites loci was 0.66 with district-specific differences (Fig. 2).

Genetic distance

Genetic distance values indicated that some of the landraces were closely related. Averages of GD over regions ranged from 0.88 between Sharqia and most of the other regions to 0.19 between Bahla and Dhank (Table 4). The assessment of genetic similarities coefficients on the regional level yielded approximately 12,880 pairs. The 161 Omani hexaploid wheat landraces ranged from 0.06 to 0.89 with a mean of 0.46. The low GS coefficient values indicate the presence of high gene diversity in Omani hexaploid wheat landrace accessions.

Cluster analysis

The GS values between accessions used to produce a dendrogramme ranged from 0.19 between Sohar and Yanqul to 0.81 between Bahla and Dhank. The accessions clustered in two groups: one group consisted of the material from Sharqia, Batinah and Dhahira comprising accessions 159SBT, 161SBT, 50DDH of the botanical variety *T. aestivum* var. *maqtaense* A. Filat. et K. Hammer, 53YDH, 90YDH, 126YDH and 158SSH (most accessions were from farmers' seed stocks). The second group was larger and divided into two subgroups of which one comprised Sharqia Sur (123SSH, 124SSH, 155WSH, 157SSH *T. aestivum* var. *pseudohostianum* (Flaksb.) Mansf.). However, the analysis could not group the accessions according to districts. This was particularly true for accessions from Dakhilia which were scattered and mixed with accessions from other districts (Fig. 3).

Principal component analysis

The analysis for the ten collection regions separated the accessions into two clearly separated groups with Sur and Yanqul in the first quadrant and the other regions in the third quadrant (Fig. 4). The first three principal components had Eigenvalues of 47.7, 5.1 and 3.3%. The

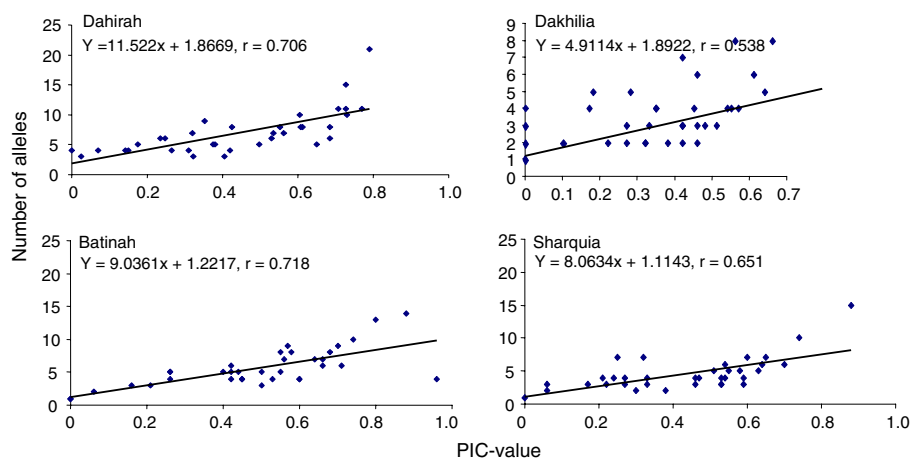
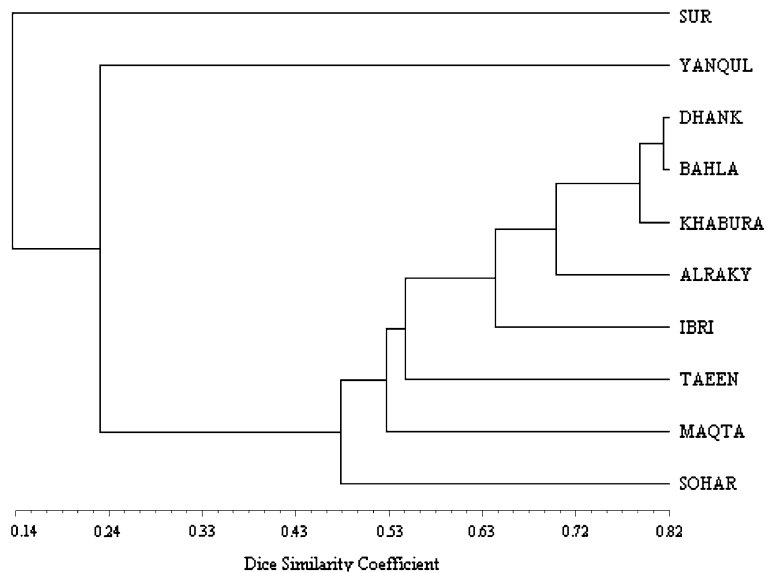


Fig. 2 Correlation between gene diversity and the number of alleles over 35 microsatellite loci in hexaploid wheat landraces. The accessions were analyzed separately for

their collection districts in Oman (Dhahira, Batinah, Sharqia and Dakhilia)

Table 4 Nei's gene distances between the different collection regions of hexaploid wheat landraces from Oman

Region	Sur	Yanqul	Dhank	Bahla	Ibri	Sohar	Khabura	Maqta	Al Raky	Taeen
Sur										
Yanqul	0.88									
Dhank	0.86	0.79								
Bahla	0.88	0.76	0.19							
Ibri	0.88	0.76	0.41	0.35						
Sohar	0.86	0.81	0.49	0.49	0.46					
Khabura	0.88	0.73	0.22	0.21	0.36	0.50				
Maqta	0.85	0.85	0.46	0.41	0.54	0.61	0.42			
Al Raky	0.80	0.78	0.31	0.28	0.33	0.49	0.31	0.47		
Taeen	0.88	0.70	0.43	0.42	0.54	0.60	0.43	0.55	0.45	

Fig. 3 Dendrogram of Omani landraces accessions grouped for ten regions of Oman according to UPGMA using Dice's similarity coefficients

results of PCA of the individual accessions showed the distribution of the landrace accessions spreading in three quadrants only. Some of Sharqia's accessions were relatively grouped and distanced from the others. Accessions from Batinah, Sharqia and Dhahira clustered together in two quadrant boxes (Fig. 5).

Discussion

In this study 35 microsatellites revealing 305 alleles from the 161 hexaploid wheat landraces were enough to discriminate all accessions. These results are in contrast with the minimum number of alleles reported by Zhang et al. (2002) who suggested a minimum of 350–400 alleles were

needed to detect genetic relationships among common wheat varieties (Zhang et al. 2002). They examined 43 Chinese wheat varieties with 90 polymorphic SSR to determine the minimum number of alleles required to detect genetic relationships in their accessions. In a study of the French bread wheat, however, a set of 41 wheat microsatellite markers (WMS) was enough to detect 609 alleles from 559 landraces and registered varieties (Roussel et al. 2004).

The average allele number obtained in the present investigation of Omani hexaploid wheats was 8.70. This compares well with previous results on genetic diversity of wheat using microsatellite analysis. Khlestkina et al. (2004) detected average allele numbers of 6.6 in 54 common spring wheat varieties and Prasad et al. (2000) found

averages allele numbers of 7.4 in 55 varieties. Manifesto et al. (2001) reported an average allele number of 10.5 from 500 European wheat varieties, whereas Huang et al. (2002) investigated with microsatellites nearly 1,000 accessions of hexaploid wheat originating from all over the world and thereby recorded an average allele number of 18.1.

The average gene diversity (PIC) obtained in the present investigation was comparable with previous results on genetic diversity of wheat using microsatellite analysis. Khlestkina et al. (2004) found a PIC-value of 0.70 in 54 common spring wheat varieties, while Prasad et al. (2000) reported a PIC-value of 0.71 in their 55 elite wheat genotypes. Analysing 105 Argentinean wheat varieties, Manifesto et al. (2001) reported an average gene diversity (PIC) of 0.72. For 500 European and world-wide collected wheats Röder et al. (2002) and Huang et al. (2002) found respective PIC values of 0.67 and 0.77. The highly significant ($P < 0.001$) correlation coefficient of 0.635 between gene diversity and number of alleles per locus for the 161 cultivated landraces (Fig. 2) confirms previous findings by Huang et al. (2002) and Roussel et al. (2004). However, it contradicts results of Prasad et al. (2000) who reported that the PIC value was uncorrelated with the number of alleles in their material.

The relatively large number of rare alleles in Batinah and Sharqia may be due to the sample size or modern commercial activities. High frequencies of rare alleles have also been reported in *Triticum urartu* Thun. ex Gandil. (Moghaddam et al. 2000), in *Aegilops tauschii* Coss. (Dudnikov 1998), in European wheat varieties (Röder et al. 2002) and for the Gatersleben wheat collection (Huang et al. 2002). Similarly, Roussel et al. (2004) reported that on average about 72% of the total number of alleles had a frequency lower than 5% and were therefore considered as rare.

The cluster analysis discriminated most of the hexaploid landraces accessions in our study. However, it did not group the landraces according to their geographic location. Similar results were obtained by Khlestkina (2004) for old and modern Siberian spring wheat varieties. Also Huang (2002) reported that not all accessions originating from the same region clustered in the same group,

indicating that the genetic diversity of *T. aestivum* is not completely related to geographic distribution. In contrast, Alamerew et al. (2004) reported that all of his accessions could be separated, clustering in two large groups.

The results of our study might also show the effects of seed exchange between farmers within or even between districts. The Sharqia data indicated a high genetic diversity within a district which may reflect the effects of cultural isolation and distinct agricultural practices. On the other hand there is the observation that farmers will give different names to wheat landraces based on their agronomic performance or minor phenotypic differences regardless of the outcome of morphological or molecular genetic studies.

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