Genetic Diversity in the Batini Barley Landrace from Oman: I. Spike and Seed Quantitative and Qualitative Traits

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ABSTRACT

The Batini landrace of barley (*Hordeum vulgare* L.) is endemic to the coastal Batinah region of Oman. Although it is important to subsistence farmers, it is threatened by increasing salinity and replacement by high yielding cultivars. Seven bulk seed samples (subpopulations) of the Batini landrace were collected from farmers' fields, which provided a germplasm collection of 3191 accessions. The objectives of this study were to characterize these accessions for spike and seed qualitative and quantitative traits, quantify phenotypic diversity, and explore significant variation in seed and spike morphological traits for future selection and breeding. Variation for 26 morphological traits was assessed among the progeny of 3191 single spikes. Phenotypic diversity indices (H') differed significantly among traits and subpopulations. Weighted H' average for subpopulations was 0.501; it ranged from 0.154 for spike glaucousness to 0.853 for number of spikelets per spike. Differences in phenotypic frequencies for 20 traits were sufficient to discriminate between subpopulations. Total genetic variation (H_T) for quantitative (0.717) and qualitative (0.533) traits differed significantly. Variance component due to subpopulations was significant for seven quantitative and 12 qualitative traits, and the within-subpopulation variance component decreased in the order: qualitative (82.12%) > quantitative (78.34) > spike-related (68.50) > grain-related (67.25) traits. Total genetic variation and genetic differentiation estimates for qualitative traits were 25% lower than for quantitative traits. Strong, nonrandom trait associations among four seed phenotypic markers showed a hierarchical pattern, indicating an adaptive response to environmental conditions and human selection. The long history of in situ conservation of this landrace in a multitude of subsistence farming systems, undoubtedly, contributed to the high variability.

Barley is one of eight founder crops of Old World agriculture (Zohary and Hopf, 1993, p. 278); the landraces of which are the evolutionary link between wild barley (*Hordeum spontaneum* K. Koch) and modern barley cultivars. Barley landraces are genetically heterogeneous populations comprising inbreeding lines and hybrid segregates generated by a low level of random outcrossing in each generation (Nevo, 1992). Moreover, having evolved across thousands of years in a multitude of environments and local farming systems, these landraces have developed abundant patterns of variation and would represent a largely untapped reservoir of useful genes for adaptation to biotic and abiotic stresses (Brush, 1995).

Landraces comprise the major genetic resource of cultivated barley in countries like Ethiopia (Alemayehu and Parlevliet, 1997), Iran (Brown and Munday, 1982), Jordan (Jaradat et al., 1987), Sardinia (Papa et al., 1998), Syria (Ceccarelli et al., 1987), and Turkey (Brush, 1995). Although these countries comprise a sizable part of barley's center of diversity, the land area under landraces is declining (Hammer et al., 1996). Almost 50% of all accessions maintained in ex situ collections are advanced cultivars or breeders' lines (Hammer et al., 1999), while landraces make up about 30% of these collections. One of the consequences of ex situ conservation is the loss of genetic diversity due to genetic drift after rejuvenation and seed increase cycles. The concomitant shift in population genetic structure on rejuvenation of old collections (Parzies et al., 2000a) emphasizes the need for in situ conservation of landraces and old cultivars (Brush, 1995)

Current theories (Willcox and Tengberg, 1995) suggest that barley was introduced into Oman and the southern parts of the Arabian Peninsula through trade between cultures of old Mesopotamia and other parts of the Persian Gulf. Undoubtedly, it underwent evolutionary modification resulting from artificial selection and adaptation to the harsh environment (Zohary and Hopf, 1993, p. 278). Carbonized rachis and seed of domesticated two-row and six-row barley and wheat (*Triticum aestivum* L.) were found in archaeological sites in southern Arabia dating back to about 5000 BP. Inscriptions were also found at a later date (about 3500 BP) indicating that wheat and barley, among other crops, had been brought down from southern Mesopotamia to this part of the Arabian Peninsula (Potts, 1993).

Barley is traditionally grown in a mixture with alfalfa (*Medicago sativa* L.) as fodder in the coastal parts of Oman. The land area under barley is about 250 ha, almost 30% of which is in the coastal Batinah region, and the remaining 70% is scattered in the mountainous regions of the country. Landholdings are very small (1–2 ha, on average) with a mean grain yield of about 300 kg ha^{-1} (Guarino, 1990).

The Batini landrace of barley is grown along the coast of Oman as a dual-purpose or forage crop and, occasionally, as a grain crop for animal feed and human consumption in the remote mountainous regions of Oman (Guarino, 1990). This six-row landrace is endemic to the Batinah region of Oman, which is a low-lying alluvial plain extending for about 240 km from Muscat to the border of the United Arab Emirates, and stretching for about 30 km inland from the coast (Guarino, 1989). Mean annual temperature in this region is about 29.0°C, while maximum temperature may reach 50.0°C.

Very little is known about the genetic diversity and morphological variability present in this landrace in Oman, a country experiencing loss of biodiversity, espe-

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cially in the Batinah region, because of replacement of landraces with modern cultivars, increasing salinity, and decreasing fresh water resources for irrigation (ICBA, 2000, p. 38). Oman was singled out (Chapman, 1985) as one of the most important remaining sites for germplasm collection in southwest Asia during the late 1980s. To fill this gap, Guarino (1989, 1990) collected 51 barley landrace accessions as a part of a larger collection (510 accessions and 58 species). However, the National Plant Germplasm System (NPGS, 2003) lists only 16 accessions of Omani barley introduced from Oman during the early 1990s.

Although farmers may have several socio-economic incentives to replace landraces with modern introduced varieties (Kebebew et al., 2001), this landrace is still being cultivated by subsistence farmers in Oman and the adjacent regions of the United Arab Emirates because of its high adaptability and tolerance to salinity (ICBA, 2000, p. 38). Nevertheless, the continued cultivation of this landrace and other indigenous crop genetic resources of Oman are potentially threatened and could be lost before they are adequately collected and thoroughly evaluated (Cromwell, 1996).

This paper is the first of a series of four papers on phenotypic and genetic diversity in the Batini barley landrace from Oman. Objectives of this part of the study were to: (i) characterize a barley germplasm collection for spike qualitative and quantitative traits, and (ii) quantify the phenotypic diversity and explore significant variation for future exploitation in selection and breeding.

MATERIALS AND METHODS

In 1999, a barley seed collection from the Batinah region of Oman (Fig. 1, map of Oman) was acquired by the International Center for Biosaline Agriculture (ICBA) and was comprised of seven bulk samples. Seed multiplication and plant selection, on the basis of readily observable plant and spike morphological and phenological traits during the 1999-2000 cropping season, resulted in a refined selection of 3191 single spikes representing seven distinctively different subpopulations (ICBA, 2000, p. 38).

Seed increase (spike to row) was performed for the selected germplasm during the 2000-2001 cropping season at the Experiment Station of ICBA (25° 13′ N and 55° 17′ E). For the purpose of this study, main tiller spikes of 3191 mature plants were characterized for a total of seven quantitative and 19 qualitative traits (Table 1). Variation within and among subpopulations was evaluated via analysis of variance (ANOVA) of measurements of individual spikes. Because of the large size of the data matrix (>22 000 data points of 3191 accessions and seven quantitative traits), normality of the data was determined from frequency plots and normality plots of the residuals obtained from the ANOVA analyses. Mean separation for each trait was performed on subpopulation means using Duncan Multiple Range Test (DNMRT) at the 0.05 level of probability.

The multivariate discriminant analysis (Table 2), followed by a jackknife validation procedure, was used on the data matrix to verify results of phenotypic selection and the separation of accessions into their respective subpopulations. The misclassified accessions were removed from further statistical analyses.

The mean and standard deviation calculated for the seven quantitative traits and for all subpopulations were used to classify accessions into three discrete categories [i.e., (i) $\leq$ mean $-$ 1.0 s.d., (ii) $>$ mean $-$ 1.0 s.d. $<$ mean + 1.0 s.d., and (iii) $\geq$ mean + 1.0 s.d.] according to Zar (1996). For the discrete multivariate log-linear analysis of the cross-classified categorical data, this method of grouping was considered more appropriate than the classification based on 33rd and 67th centiles (Agresti, 1990).

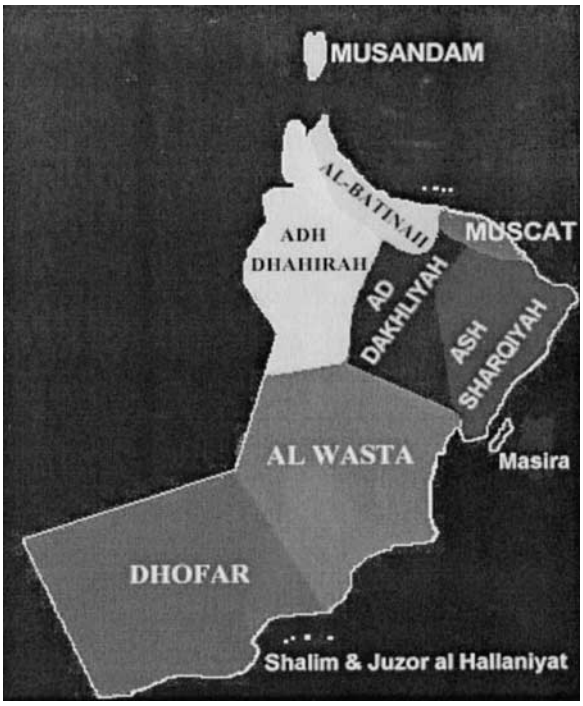

Fig. 1. Map of Oman showing the Batinah administrative district where barley landrace was collected.

Frequency data for discrete qualitative and quantitative traits were used to carry out: (i) the Kruskal-Wallis test statistic, as described in Zar (1996), to estimate the power of the qualitative and quantitative traits for discrimination among subpopulations, (ii) discriminant analysis among the seven subpopulations, determined on the basis of discrete qualitative and quantitative traits with significant P values in the Kruskal-Wallis test, (iii) estimate the phenotypic diversity index, total diversity and level of differentiation for each subpopulation and trait, and (iv) estimate mean gene diversity, mean number of alleles (categories) per locus, and percentage of polymorphic loci by the 5% criterion for each subpopulation.

The polymorphic index, as described by Zhang and Allard (1986), was calculated from relative frequencies of the 19 qualitative, seven discrete quantitative traits and seven subpopulations. The adjustment in phenotypic diversity indices suggested by Zar (1996) was implemented to account for differences in the number of phenotypes (range from 2–4), and testing for differences between two diversity indices was performed according to Hutchison (1970).

Phenotypic Diversity Analyses

Frequency data for each quantitative trait, groups of quantitative or qualitative traits, and for each subpopulation were used to calculate the following statistics according to Nei (1973, 1987): gene diversity for each phenotypic marker, H; mean number of alleles per locus, A; effective number of phenotypic markers per locus; percent polymorphic loci, $P(0.05)$; total gene diversity, H_T; and genetic differentiation, G_{ST}.

Table 1. Number of observed (and effective) phenotypes for 21 qualitative and seven quantitative traits, ANOVA and variance components in phenotypic diversity indices, and *P* values for seven subpopulations (SP) of the Batini barley landrace from Oman.

Trait	Data type	Phenotypes used in correspondence analysis	Number of observed and (effective) phenotypes	Phenotypic diversity index	Percent significant differences among SPs, $N = 21$	Percent variance due to SPs	*P*-Kruskal-Wallis test (6 df)
Awn length compared to spike length	Q†	An-1‡	3 (2.5)	0.425*	38.0	32.0	0.03
Awn length	C		3 (1.35)	0.554**	66.7	54.3**	0.01
Awn spread.	Q	An-2	3 (3.0)	0.524**	52.4	45.0*	0.02
Awn: anthocyanin coloration of tips	Q		4 (1.7)	0.231*	33.0	25.8	0.08
Awn roughness	Q	An-3	2 (1.5)	0.698**	76.2	59.8**	0.01
Glume hairiness	Q	Gl-1	2 (1.4)	0.356*	14.3	18.9	0.15
Lemma color	Q	Gl-2	2 (1.9)	0.753**	80.9	65.2**	0.01
Aleurone color	Q	Gr-1	2 (1.3)	0.575**	63.8	57.9**	0.01
Grain color	Q	Gr-2	4 (3.6)	0.732**	80.9	65.8**	0.01
Grain: dorsal view	Q		3 (1.1)	0.149	0.0	9.0	0.30
Grain: lemma base type	Q	Gr-3	2 (1.3)	0.258*	23.8	24.3	0.09
Grain: rachilla hair type	Q	Gr-4	3 (2.2)	0.358*	47.6	42.9*	0.01
Grain: spiculation of inner lateral nerves	Q	Gr-5	3 (2.6)	0.562**	61.9	56.8**	0.01
Grain: length of lodicules	Q	Gr-6	3 (1.3)	0.289*	28.6	25.6	0.10
Rachis: length of first segment	Q		3 (3.0)	0.625**	85.7	72.1**	0.01
Rachilla length	Q		2 (2.0)	0.685**	80.9	68.3**	0.01
Spike attitude	Q	Sp-1	3 (1.8)	0.548**	76.2	62.7**	0.01
Spike shape	Q	Sp-2	4 (3.0)	0.783**	85.7	74.5**	0.01
Spike density	Q	Sp-3	3 (3.0)	0.805**	85.7	77.5**	0.01
Spike glaucousness	Q		3 (1.3)	0.154	14.3	19.7	0.12
Spike length	Q	Sp-4	3 (2.3)	0.782**	80.9	65.8**	0.01
Spikelets/spike	C		3 (2.9)	0.853**	80.9	78.8**	0.01
Spike weight	C	Sp-5	3 (2.37)	0.819**	85.7	78.2**	0.01
Seed weight/spike	C		3 (2.09)	0.795**	76.2	61.3**	0.01
Seeds/spike	C		3 (2.2)	0.805**	80.9	70.4**	0.01
Thousand grain weight	C		3 (2.16)	0.769**	80.9	69.5**	0.01

* Significant differences among subpopulations at the 0.05 level of probability.
** Significant differences among subpopulations at the 0.01 level of probability.
† Q = qualitative, C = quantitative data reduced to categorical.
‡ Awn-, Glume-, and Grain-related traits (An-, Gl-, and Gr-, respectively) having significant Kruskal-Wallis test statistic, used for correspondence analysis.

Log-Linear Models

The multitrait organization of phenotypic variation within the landrace for four seed qualitative traits showing variation controlled by single genes (Nilan, 1964) was analyzed by means of log-linear models (Agresti, 1990). The most parsimonious models with best goodness-of-fit to the frequency tables of the observed data sets, were obtained by model selection procedures based on the partitioning of likelihood-ratio statistics (G^2) (Agresti, 1990).

A polymorphic distance, analogous to genetic distance based on allozyme or molecular data (Nei, 1973, 1987), was calculated for the seven subpopulations by means of frequencies of qualitative, quantitative, spike-related, and grain-related traits. The total variance in each of these four groups was partitioned into its components: among and within subpopulations.

Table 2. Original number of accessions, number, and percent accessions correctly classified by discriminant analysis of seven quantitative and 19 qualitative traits measured on the Batini barley landrace from Oman.

Subpopulation	Number of accessions in original collection	Number of accessions in subpopulation after discriminant analysis	Percent correct classification
Batini 1	376	327	87
Batini 2	497	363	73
Batini 3	638	383	60
Batini 4	809	492	61
Batini 5	317	247	78
Batini 6	207	184	89
Batini 7	347	312	90
Total	3191	2308	72.3

Multivariate Graphical Analyses

The principal components analysis (PCA) was performed with the standardized mean values for each of the seven quantitative traits and subpopulation. Results of PCA were used to study the interrelationships and adjustments in the seven quantitative traits, and to detect any subpopulation groupings based on similarities in trait interrelationships and adjustments. Correspondence analysis (CA) using frequencies of the awn-, spike-, glume-, and grain-related traits was performed to reduce the dimensionality of the data matrix and to identify associations among these sets of qualitative traits. Principal Coordinate Analysis (PCoA) was performed with the inter-subpopulation dissimilarity distances as data units to identify major cluster groups and to graphically display relationships among subpopulations (Gower, 1966). In addition, frequency data per subpopulation were used to calculate squared Euclidean distances between subpopulations for subsequent unweighted pair group method with arithmetic average (UPGMA) clustering of subpopulations (Sneath and Sokal, 1973).

All statistical analyses were conducted by several modules in the statistical packages STATISTICA 6.0 (StatSoft Inc., 2001), SYSTAT 10.2 (SYSTAT Software Inc., 2002), and POPGENE 1.32 (Yeh et al., 2000), unless otherwise specified.

RESULTS

Univariate ANOVA

Summary results of the analysis of variance, mean separation, and variance component due to subpopulations of the phenotypic diversity indices for 26 traits are presented in Table 1. A total of 54 categories were ob-

Table 3. Total genetic variation (H_T) and genetic differentiation (G_{ST}) for seven quantitative traits measured on seven subpopulations of the Batini barley landrace from Oman.

Trait	H_T	G_{ST}
Spike length	0.759	0.207
Awn length	0.547	0.267
Spike weight	0.823	0.493
Spikelets/spike	0.849	0.243
Seed weight/spike	0.825	0.463
Seed number/spike	0.829	0.312
Grain weight	0.788	0.478
Mean	0.774	0.352

served for the 19 qualitative traits scored on accessions of all seven subpopulations with an average of 2.84 categories per qualitative trait. However, the mean number of effective qualitative categories per trait was 2.06, or 72.8% of the observed number. On the other hand, data reduction of the seven quantitative traits resulted in a total of 21 categories, and the average effective number of phenotypes per trait was 2.195, or 73.2% of the observed number.

Phenotypic diversity index estimates ranged from 0.149 for the grain dorsal view to >0.8 for spike-related traits. The weighted average phenotypic diversity index was 0.501; however, separate phenotypic diversity indices for quantitative (0.768) and qualitative (0.403) traits differed significantly from each other ($P < 0.01$).

Differences among subpopulations in the phenotypic diversity index were significant for 17 of the 19 qualitative, and for all seven quantitative traits. However, the magnitude of these differences among subpopulations, as expressed by the percent significant differences for all possible 21 pairwise comparisons among seven subpopulations, varied from 0.0 for grain dorsal view to 85.7% for four spike- and rachis-related traits.

The variance component due to subpopulations ranged from 9.0 for grain dorsal view to >70% for spike-related traits. Significance tests, as seen from the level of significance associated with the percent variance due to subpopulations, suggest that a sizable portion of the variability in phenotypic diversity indices for 12 qualitative and all seven quantitative traits was accounted for by differences among subpopulations. *P* values for the Kruskal-Wallis test indicate that differences in phenotypic frequencies for 13 qualitative and for all seven quantitative traits were powerful enough to discriminate between subpopulations.

Total Genetic Variation and Genetic Differentiation

Mean genetic diversity (H_T) for seven quantitative traits, across all subpopulations, averaged 0.774 and ranged from 0.547 for awn length to 0.849 for number of spikelets per spike (Table 3). The extent of differentiation between the seven subpopulations for these quantitative traits (G_{ST}) implies that, on average, 65% of the total variation for these quantitative traits is partitioned within subpopulations, with a minimum of 50.7% for spike weight to a maximum of 79.3% for spike length.

Total genetic diversity (H_T) and level of genetic differentiation (G_{ST}) in 19 qualitative and seven quantitative traits for each of the seven subpopulations are presented in Table 4. H_T for qualitative traits averaged 0.533 with a range of 0.196, whereas quantitative traits displayed a higher H_T (0.717) and a slightly narrower (0.185) range; the respective values for G_{ST} were 0.152 (0.117) and 0.2017 (0.165). H_T and G_{ST} values for qualitative traits were, on average, about 25% lower than the respective values for quantitative traits with no clear association between estimated values ($r = 0.423$, n.s., -0.116, n.s., for the H_T and G_{ST} paired values, respectively).

Table 4. Total genetic variation H_T within seven barely subpopulations and genetic differentiation G_{ST} for seven quantitative and nineteen qualitative traits found among accessions within seven subpopulations of the Batini barley landrace from Oman.

	H_T		G_{ST}	
Subpopulations	Quantitative	Qualitative	Quantitative	Qualitative
Batini 1	0.709	0.595	0.198	0.109
Batini 2	0.675	0.405	0.215	0.152
Batini 3	0.682	0.566	0.273	0.215
Batini 4	0.822	0.602	0.195	0.087
Batini 5	0.637	0.546	0.108	0.204
Batini 6	0.698	0.479	0.228	0.199
Batini 7	0.795	0.545	0.195	0.098
Correlation coefficient, r	0.423, NS		−0.116, NS	

Phenotypic Diversity Analyses

Average gene diversity (H), mean number of alleles per locus (A), and percent polymorphic loci [$P(0.05)$] for the whole collection were 0.2607, 2.06, and 0.7357, respectively (Table 5). Significant differences were detected for gene diversity among three groups of subpopulations. Batini 4 and Batini 6 had high H values, Batini 1, Batini 3, and Batini 7 had intermediate, and Batini 2 and Batini 5 had low H values. However, two groups of subpopulations displayed significant differences for A and $P(0.05)$ as indicated by the mean separation using DNMRT. Gene diversity was positively ($r = 0.583$) but not significantly ($P = 0.07$) correlated with mean number of alleles per locus, while it was positively ($r = 0.858$) and significantly ($P = 0.01$) correlated with percent polymorphic loci. On the other hand, the positive correlation ($r = 0.656$) between A and $P(0.05)$ was significant ($P = 0.05$).

Total variance estimates, using frequency data for qualitative, quantitative, spike-, and grain-related traits, were partitioned into their components: among subpopulations and within subpopulations. Average phenotypic

Table 5. Genetic diversity indices (gene diversity, *H*; mean number of alleles per locus, *A*; and percent polymorphic loci, *P*(0.05)) for seven quantitative and 19 qualitative traits within seven subpopulations of the Batini barley landrace from Oman.

Subpopulation	Gene diversity *H*	Mean number of alleles per locus, *A*	Percent polymorphic loci, *P*(0.05)
Batini 1	0.247b†	2.3a	0.85a
Batini 2	0.192c	1.9b	0.54b
Batini 3	0.243b	2.3a	0.83a
Batini 4	0.378a	2.5a	0.81a
Batini 5	0.187c	1.1b	0.46b
Batini 6	0.349a	2.1a	0.87a
Batini 7	0.229b	2.2a	0.79a
Mean	0.261	2.06	0.736

† Values within each column, followed by the same letter, do not differ significantly at $P = 0.05$.

Table 6. Summary of variance component analyses (using morphological and categorical trait frequencies) for qualitative, categorical, spike-, and grain-related traits in seven subpopulations of the Batini barley landrace from Oman.

Data type	Variance components		Mean phenotypic distance between subpopulations
	Among subpopulations	Within subpopulations	
Qualitative traits	17.88	82.12	0.378
Quantitative traits	21.66	78.34	0.489
Spike-related traits	31.50	68.50	0.457
Grain-related traits	32.75	67.25	0.503

distances between populations were calculated for each of the four data types (Table 6). The within subpopulations variance component decreased in the following order: qualitative > quantitative > spike-related > grain-related traits with a concomitant increase in the average phenotypic distance between subpopulations.

Log-Linear Models

Frequency data for four qualitative traits (aleurone color, awn roughness, lemma color, and rachilla hair), which are known to be controlled by single genes and were highly powerful in differentiating among subpopulations (*P* values for the Kruskal-Wallis Test, Table 1), were used to calculate total genetic variation and genetic differentiation in the whole barley collection (Table 7). The level of population differentiation, based on these estimates, was relatively low for lemma color (45%) and aleurone color (48%), as compared with the high values for rachilla hair (77%) and awn roughness (68%). Consequently, slightly less than half of the total variation for lemma and aleurone color, and more than two-thirds of the total variation for awn roughness and rachilla hair are partitioned within subpopulations.

Phenotypic frequencies for the same four traits were used to construct six two-way, four three-way, and one four-way contingency tables. All but one of the **U** terms are presented in Table 8. The full model (aleurone color × awn roughness × lemma color × rachilla hair) was not significant, and is not presented. All **U** values for the two-way and three-way contingency tables were significant.

Multivariate Graphical Analyses

Principal components analyses were performed on the standardized matrix of the quantitative traits for each subpopulation, thereby removing the effect of scale (Table 9). The relative magnitude of the coefficient of that trait in the principal components analysis, associating it with one of the first two principal components,

Table 7. Total genetic variation H_T and genetic differentiation G_{ST} for four traits controlled by single genes found among accessions within seven subpopulations of the Batini barley landrace from Oman.

Trait	Locus	H_T	G_{ST}
Aleurone color	*blbl* (White)/*Bl-* (Blue)	0.334	0.52
Awn roughness	*rr* (Smooth)/*R-* (Rough)	0.462	0.32
Lemma color	*B-* (black)/*bb* (White)	0.357	0.55
Rachilla hair	*S-* (Long)/*ss* (Short)	0.366	0.23

Table 8. Nonrandom associations of traits controlled by single genes at the aleurone color (1), awn roughness (2), lemma color (3), and rachilla hair (4) loci detected by estimated U-terms and their standardized values in a log-linear model, in seven barley subpopulations of Batini landrace from Oman.

U terms	Estimated U value	Standardized U value†
U12	0.54	3.51**
U13	0.89	5.62***
U23	0.29	2.77**
U123	0.19	3.59**
U14	0.98	6.56***
U24	0.31	5.33***
U124	0.54	2.37**
U34	0.72	2.88**
U134	0.38	2.98**

** Denotes that the observed genotypic frequencies deviated from independence at the 0.01 level of probability.
*** Denotes that the observed genotypic frequencies deviated from independence at the 0.001 level of probability.
† Standardized U terms are standardized normal variables with zero mean and unit variance under the null hypothesis of complete independence.

was used to assign it to one of these two components. The first and second principal components, on average, explained 49.8 and 26.9% of the total variation in the seven subpopulations, respectively. Specific patterns were identified in the way traits were associated to form the first or second principal components. Number of spikelets per spike, number of seed per spike, and spike length (except for Batini 2) had high loadings on, and were associated with, PC1. On the other hand, 1000-kernel weight and awn length (except for Batini 4) had high loadings on, and were associated with, PC2. Finally, spike weight and seed weight (except for Batini 4 and Batini 6) had high loadings on, and were associated with, PC1.

The most important traits found to explain the variation, in the combined PCA for all subpopulations, were seed weight, 1000-kernel weight and number of seed per spike for PC1, and spike length and number of spikelet groups per spike in PC2. PCA1 and PCA2 explained 63.23 and 19.15% of total variation, respectively (Fig. 2), and separated subpopulations into four groups (Fig. 3) depending on the magnitude of trait loadings.

Correspondence analysis (CA) separated 16 spike-, awn-, grain-, and glume-related phenotypic traits (Fig. 4) into two groups. The grain- and glume-related traits grouped together and were separated from the awn- and spike-related phenotypic traits by the first and second CA axes. Four patterns of association were detected among the eight glume and grain qualitative traits: (i) aleurone (Gr-1) and grain colors (Gr-2); (ii) spiculations of inner lateral nerves (Gr-5) and length of lodicules (Gr-6); (iii) glume hairiness (Gl-1) and rachilla hair type (Gr-4) were plotted in pairs in close proximity; and (iv) lemma color (Gl-2) and lemma base type (Gr-3). Although separate from the other three grouping, the first was in the proximity of the Gl-1/Gr-4 group, whereas the second was totally separate.

Three spike- and awn-related traits were plotted opposite from, and mirrored the grain- and glume-related traits on the positive sides of the CA axes. These were first, awn length (An-1) and spike attitude (Sp-1); second, awn spread (An-2) and awn roughness (An-3); and

Table 9. Association of seven quantitative traits with, and cumulative variance explained by, two principal components (PC1 and PC2) for each of seven subpopulations of the Batini barley landrace from Oman.

Subpopulation	Spike length	Awn length	Spike weight	Seed weight	Spikelet number	Seed number	TKWT	Percent variance explained by		Total variance explained (%)
	With high loading on PC							PC1	PC2	
Batini 1	1	2	1	1	1	1	2	51.07	25.78	76.85
Batini 2	2	2	1	1	1	1	2	53.87	22.25	76.12
Batini 3	1	2	1	1	1	1	2	45.52	28.78	74.30
Batini 4	1	1	2	2	1	1	2	42.65	32.31	74.96
Batini 5	1	2	1	1	1	1	2	52.97	26.27	79.24
Batini 6	1	2	2	2	1	1	2	50.37	27.76	78.13
Batini 7	1	2	1	1	1	1	2	51.86	25.13	76.99

third, spike shape (Sp-2), spike density (Sp-3), spike length (Sp-4), and spike weight (Sp-5).

UPGMA cluster analysis and PCoA generated two similar graphs (Fig. 5 and Fig. 6, respectively), each with two sets of subpopulations. UPGMA cluster analysis separated the seven subpopulations into two separate groups at a linkage distance of 0.44. Member subpopulations within each group were also separated at linkage distances ranging from 0.17 to 0.36, with Batini 2 and Batini 3 being the closest, and Batini 4 the farthest. The first axis of the PCoA accounted for 53.54% of total variation and separated Batini 3, Batini 2, Batini 7, and Batini 4, in this order, from the remaining three subpopulations (Fig. 6). The second axis accounted for 18.2% of total variation and separated Batini 1, Batini 3, Batini 2 and Batini 6, in this order, from the remaining three subpopulations.

DISCUSSION

Indigenous farming communities in developing countries contributed, for millennia, to the evolution, enrichment, and in situ conservation of crop landraces. These include, but are not limited to, barley (Ceccarelli et al., 1987), sorghum [*Sorghum bicolor* (L.) Moench) (Dje' et al., 1998), teff [*Eragrostis tef* (Zuccagni) Trotter] (Kefyalew et al., 2000), and pearl millet [*Pennisetum glaucum* (L.) R. Br.] (Busso et al., 2000); however, little has been done to understand the intraspecific diversity in their subsistence agricultural ecosystems (Busso et al., 2000).

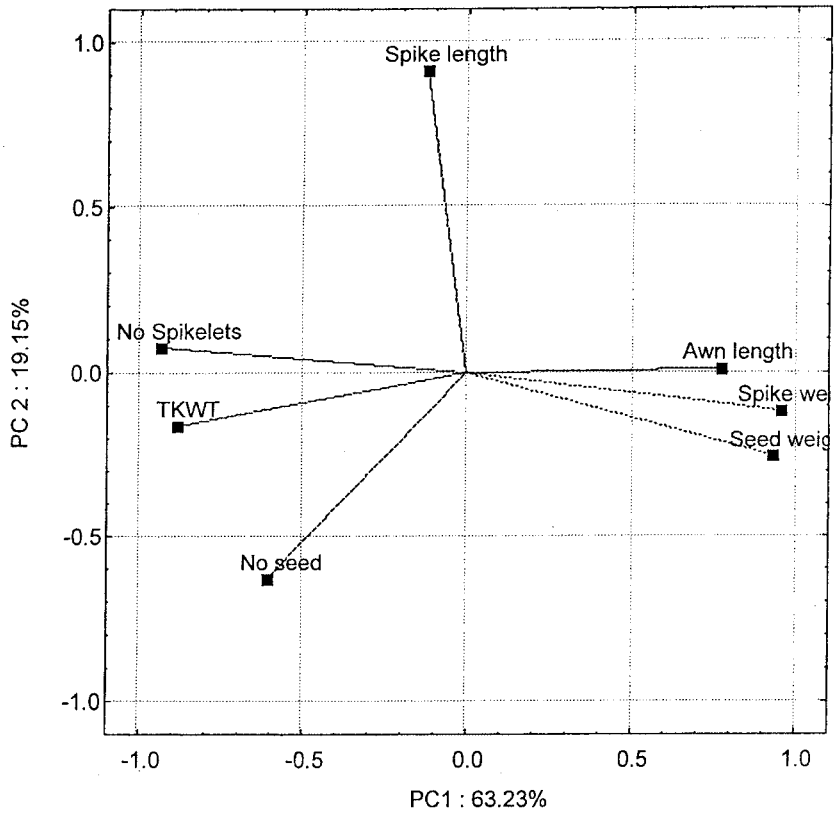

Fig. 2. Principal component analysis (PCA) plot for seven quantitative traits measured on accessions of seven subpopulations of the Batini barley landrace from Oman.

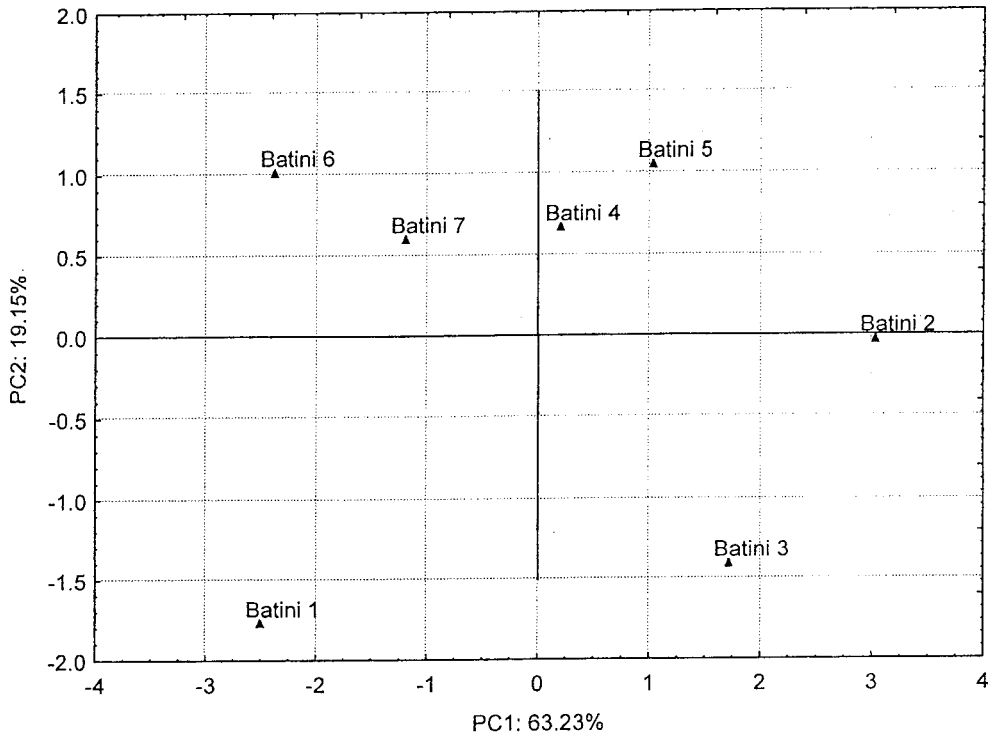

Fig. 3. Principal component analysis (PCA) plot for seven subpopulations of the Batini barley landrace from Oman, based on seven quantitative traits.

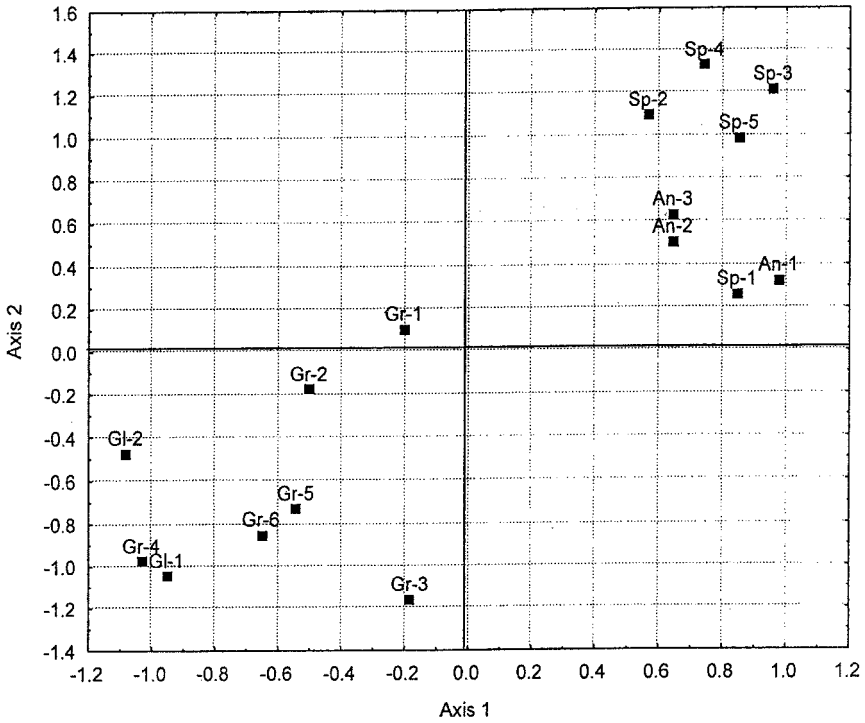

Fig. 4. Correspondence-analysis plot of 16 Awn-, glume-, grain-, and spike-related traits in the Batini barley landrace from Oman. (See Table 1 for abbreviations).

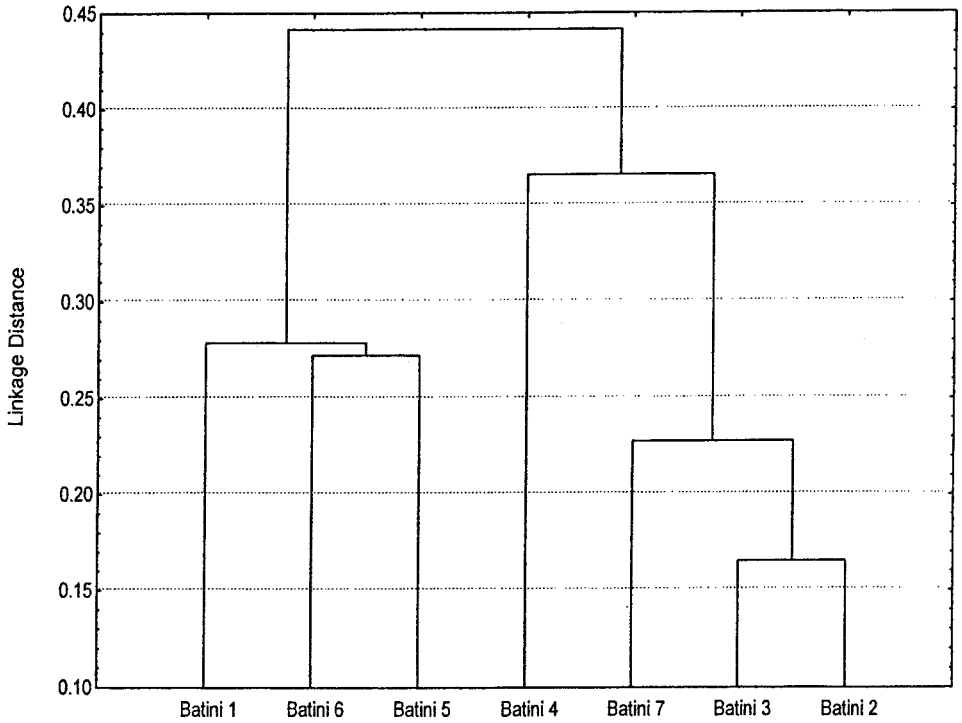

Fig. 5. Unweighted pair group method with arithmetic average (UPGMA) clustering based on squared Euclidean distances among seven subpopulations of the Batini barley landrace from Oman.

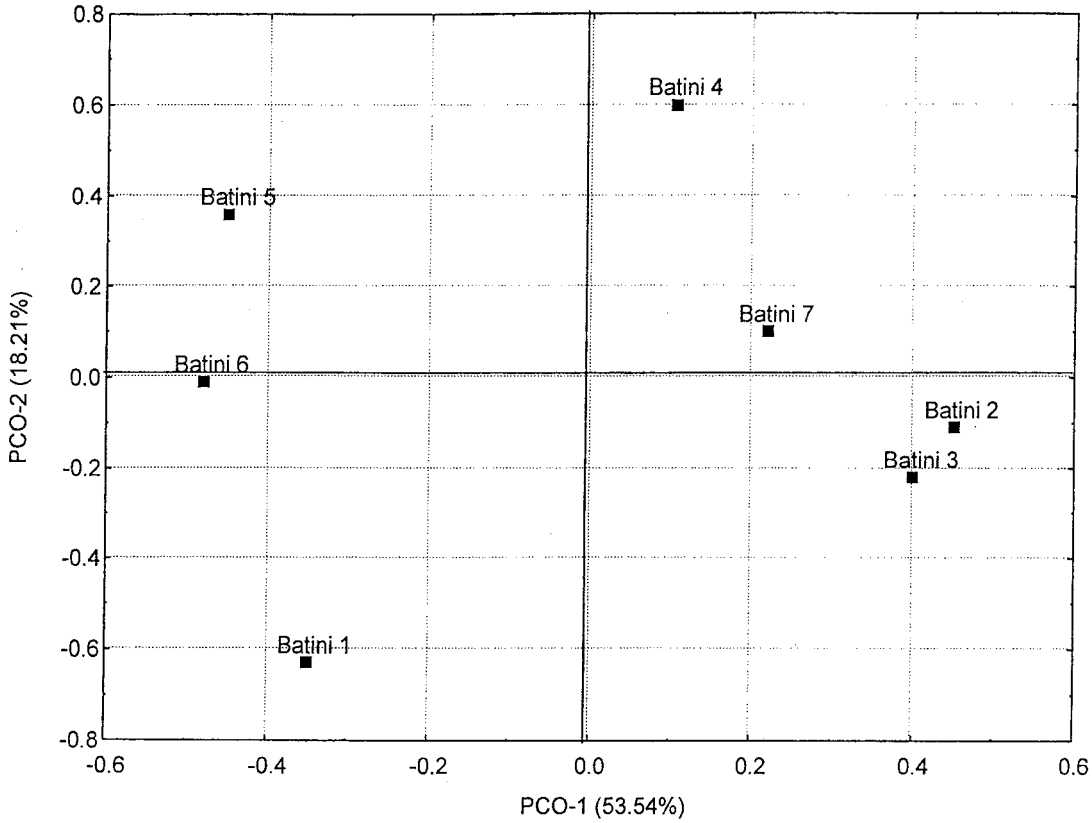

Fig. 6. Principal coordinates plot of the diversity, based on seven categorical and 19 qualitative traits, for seven subpopulations of the Batini barley landrace from Oman.

Most likely, the Batini landrace evolved over many generations through the long process of natural and conscious selection (Harlan, 1968), in a multitude of local irrigated farming systems involving date palm (*Phoenix dactylifera* L.), alfalfa, and vegetable crops (Guarino, 1989, 1990). It is highly likely that desirable plant traits, conducive to development and survival under the harsh climatic conditions of the southern parts of the Arabian Peninsula, are available with high frequencies in this landrace.

Phenotypic Diversity Analyses

The analyses described in this paper could have been more informative had the exact geographical source of each original seed sample been known, and had individual spike or plant samples been kept separate (DeLacy et al., 2000). Although not all qualitative and quantitative traits in this study are of direct agronomic importance, most (seven quantitative traits and at least six qualitative traits) are typically used in germplasm characterization for useful attributes (Koebner et al., 2002). In addition, these morphological traits have been chosen on the basis of their usefulness for distinctness testing in barley (Lakew et al., 1997).

The high level of phenotypic diversity in this single landrace ($H' = 0.501$) is comparable to, or higher than, phenotypic diversity levels reported for larger germplasm collections of landraces in the barley primary (e.g., Brown and Munday, 1982; Jaradat et al., 1987; Parzies et al., 2000a) and secondary (e.g., Demissie and Bjornstad, 1996) centers of genetic diversity. Brown and Munday (1982) reported a very low average phenotypic diversity index ($H' = 0.156$) for the same phenotypic loci as listed in Table 7 in 12 landrace populations, presumably because of low variability for two phenotypic markers (*vv* and *B*-), as compared with 0.287 in 11 Syrian (Parzies et al., 2000a), and with 0.534 on the basis of nine phenotypic markers in Ethiopian (Kebebew et al., 2001) landraces. However, it was argued (Bjornstad et al., 1997) that phenotypic diversity does not reflect a random and chromosomally balanced sample of genetic variation. Therefore, this high phenotypic diversity may not reflect a higher average diversity at biochemical or molecular levels (Lefebvre et al., 1993). Nevertheless, the "functional genetic diversity" (i.e., based on morphological traits deliberately targeted for selection by farmers) (Koebner et al., 2002), and population differentiation (based on phenotypic markers) were found to be higher when compared with biochemical markers in cultivated barley (Jaradat et al., 1987), *Plantago* (Wolff, 1991), wheat (Tsegaye et al., 1996), and sorghum (Dje' et al., 1998). Moreover, Donini et al. (2000) and Koebner et al. (2002) found, in a detailed study of genetic diversity in wheat and barley varieties released in the UK during the 20th century, that the average diversity per trait for four biochemical and molecular traits was only 20 to 70% of the average diversity per morphological trait; these differences were attributed to the multigenic nature of most individual phenotypic markers, and hence variation at more than one locus is being analyzed.

The simply inherited morphological traits (Table 1) have been used to assess genetic diversity in barley and for testing the distinctiveness and uniformity of barley landraces (e.g., Brown and Munday, 1982; Alemayehu and Parlevliet, 1997; Kebebew et al., 2001) and germplasm collections (Allard, 1992). Allelic frequencies, at least for four traits (Table 7), were assumed to be equal to phenotypic frequencies based on results of parallel analysis of multilocus outcrossing rates in two barley landrace populations from Syria (Parzies et al., 2000b).

Selection by farmers and natural selection may have resulted in the high frequency of certain phenotypes adapted to the prevailing climatic and edaphic conditions (Ceccarelli et al., 1987), with farmers actively selecting for certain phenological (e.g., earliness) and agronomic (e.g., plant height, tillering capacity, grain color, grain yield and forage yield) traits (Kebebew et al., 2001).

Farmers distinguish the barley varieties by phenotypic markers, such as spike length, spike density, and spike attitude (Negassa, 1985b). The overall shape of the spike is determined, in part, by the spacing of the mature kernels on the rachis, which in turn, is greatly influenced by the rachis internode. All spike-related traits (i.e., attitude, shape, density, length, and rachis internode as expressed by number of spikelets per spike) displayed high levels of phenotypic diversity and were instrumental in separating subpopulations in multivariate analyses (Table 9, Fig. 3, 5, and 6).

Grain color is the most important selection criterion used by farmers to classify barley landraces and varieties (Ceccarelli et al., 1987; Parzies et al., 2000a; Kebebew et al., 2001). Demissie and Bjornstad (1996) suggested that human selection against pigmented barley strains might be responsible for the high frequency for the white kernel phenotype. A high number of functional phenotypes (3.6 or 90% of observed number), a high phenotypic diversity index (0.732), and the high variance component due to differences among subpopulations (65.8%) all point to the high level of variation for this trait in the Batini landrace.

Rachilla length is considered (Nilan, 1964) as one of the best taxonomic characteristics in barley; however, its adaptive significance is not yet known (Kebebew et al., 2001). Apparently (Negassa, 1985b), there is no selection pressure by farmers targeting this trait, as the short phenotype maintained a high frequency (about 70%) in the Batini and other barley landraces from Ethiopia (Demissie and Bjornstad, 1996). Both phenotypes (short and long) were represented in all subpopulations; however, subpopulation four has a higher than average frequency of the short (*ss*) phenotype (67.4%).

Glume hairiness is a heritable trait and was found to be associated with resistance to karnal bunt [caused by *Tilletia indica* Mitra = *Neovossia indica* (M. Mitra) Mundk.] (Warham, 1988) and powdery mildew [caused by *Erysiphe graminis* DC. f. sp. *hordei* Em. Marchal = *Blumeria graminis* (DC.) E. O. Speer] (Negassa, 1985a). It appeared with high frequencies (65–70%) in two subpopulations (Batini 1 and Batini 6) in this study and in

most Ethiopian barley landraces (Kebebew et al., 2001). Undoubtedly, farmers have used it to identify and classify barley landrace varieties. It displayed a relatively low phenotypic diversity index in this study (0.356) because of the high frequency of the hairy phenotype in two subpopulations.

Diversity among and within Subpopulations

Lakew et al. (1997) remarked that variation for genotypic and phenotypic markers among plant populations can be from nine to 40 times higher than the variation within populations, depending on the trait and location of testing. Given the breeding system of barley (Hamrick and Godt, 1997), genetic variation is expected to be higher among than within populations. Several studies on barley landraces (e.g., Brown and Munday, 1982; Parzies et al., 2000a) indicated that 40 to 50% and 50 to 60% of the total genetic variation captured resides among and within landraces, respectively. In comparison, wheat (Donini et al., 2000) and barley (Koebner et al., 2002) varieties grown in the UK during the 20th century were monitored for their temporal flux of diversity in morphological and molecular traits. These researchers found that, in wheat, 10 and 90% of the total variation was partitioned among and within varieties, respectively; the respective values for barley varieties were 15.1 and 84.9%.

In the current study, average H_T and G_{ST} estimates for all traits combined are in line with values quoted for barley landraces, with 40.5 and 59.5% of total genetic variation being partitioned among and within subpopulations, respectively. In comparison, 12 Iranian (Brown and Munday, 1982), two Syrian (Parzies et al., 2000a), and 28 Syrian and Jordanian (Ceccarelli et al., 1987) barley landraces partitioned 55, and 45%, 55.3 and 44.7%, and 40.5 and 59.5% of total variation for variable numbers of phenotypic markers among and within populations, respectively. On the other hand, H_T and G_{ST} estimates deduced from data on six morphological traits (row type, caryopsis cover in addition to the four phenotypic markers listed in Table 7) and 51 accessions of Ethiopian barley landraces (Demissie and Bjornstad, 1996) were 0.572 and 0.428, respectively.

It was argued (Koebner et al., 2002) that morphology-based G_{ST} values are more likely to generate a biased picture of diversity trends than the biochemical and molecular marker-based G_{ST} values because phenotypic markers can be deliberately targeted for selection by farmers. Nonetheless, subsistence farmers have to keep seed of their barley crop for the next year at a seeding rate of 50 to 120 kg ha^{-1} (Alemayehu and Parlevliet, 1997). They may not exercise conscious selection of specific plant type(s), and consequently seed of a large number of single, and highly variable, plants is used to grow the next crop. The exceptionally high within-landrace variation levels, found in this and other studies, is maintained, if not maximized, by a combination of genetic, environmental, and management factors.

Parzies et al. (2000a) observed a gradual and significant decline in average gene diversity, number of alleles per locus, and percentage of polymorphic loci, with a concomitant increase in genetic differentiation in barley landraces as time in ex situ storage increased. Consequently, the best protection against the loss of within landrace variation would be in situ conservation (Swanson, 1996) and the collection and maintenance of individual plants within a landrace.

Log-Linear Analysis

The pronounced nonrandom associations among, at least, four spike traits controlled by single genes (Table 7) in the whole collection may reflect either farmers' conscious selection, or an association between phenotype and utility of the grain (Kebebew et al., 2001). The persistence, during the adaptive development of landraces, of these and similar associations reported on barley landraces from Iran (Brown and Munday, 1982), Ethiopia (Asfaw, 1989; Demissie and Bjornstad, 1996), and Syria (Parzies et al., 2000a), could be due to an adaptive response to similar environmental conditions, but, nevertheless, molded by human selection (Ford-Lloyed et al., 2001).

All **U** values for the two-way and three-way contingency tables were significant (Table 8), implying that the nonrandom associations among alleles at these loci, generally, have a hierarchical pattern. Strong pairwise and three-way associations between all possible gene pairs may suggest that the pairwise associations are contingent on the presence of alleles at the third locus (Li and Rutger, 2000).

Multivariate Graphical Analyses

Multivariate analyses when applied to the set of 26 quantitative and qualitative traits of the Omani barley landrace were successful in discriminating among different subpopulations, and in discerning groups of quantitative and qualitative traits with similar loadings or discriminating power among these subpopulations.

PCA, when applied to single or multiple subpopulations, in two principal components, accounted for most (79.66 and 82.38%, respectively) of total variation. With 71.75% of the variation accounted for by the first two axes in the PCoA, the separation of the seven subpopulations was possible on the basis of multiple qualitative and quantitative traits. PCA operated on the correlation matrix between the seven quantitative variables, and determined the linear combinations that accounted for the greatest proportion of the variation in the data set. PCoA, on the other hand, operated on the similarity matrix or distance matrix between subpopulations, and determined the coordinate vectors that accounted for the greatest proportion of the total distance between subpopulations (Busso et al., 2000). PCoA reduced the multidimensionality of the data to a form where qualitative differences in diversity among subpopulations can be visualized. PCoA results confirmed those obtained by UPGMA cluster analysis. Several studies identified similar trait associations of spike- and seed-related morphological markers in factor (Jaradat et al., 1987) and principal component (Ruiz et al., 1997) analyses.

CONCLUSION

Landrace cultivation has been discouraged in many developing countries because of low yield potential and susceptibility to diseases. Although exotic barley cultivars out-yield local landraces under good management practices in selected testing sites (Ceccarelli et al., 1987), local landraces usually out-yield the exotic material under the low input conditions that predominate in subsistence farming systems. For such conditions (Lakew et al., 1997), native germplasm should be exploited to improve productivity.

The phenotypic and statistical evidences reported in this study indicate that farmers' selection for desirable agronomic traits is a major force shaping the dynamics of crop plant populations in subsistence agriculture in many parts of the developing world. Consequently, the in situ conservation of these landraces ensures the continuation of this dynamic process.

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