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How diverse a farmer-managed wheat landrace can be?

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Abstract

Phenotypic variation in phenological, quantitative and qualitative traits was assessed in geographically-isolated, farmer-managed wheat landrace populations grown under subsistence farming conditions. Several multivariate, genetic diversity and structural equation modeling procedures were used to build a comprehensive structure of the landrace and to (1) identify and construct multivariate distances between components of the landrace, (2) identify plant- and seed-related traits contributing to its composition, (3) build principal components that can account for maximum variation, (4) quantify variance components accounted for by major seed qualitative traits, (5) partition total diversity and estimate levels of population differentiation, (6) build and validate a predictive model of landrace population-trait association, (7) identify traits affecting spikelet fertility as a critical component of grain yield under the prevailing hot conditions in Oman, and (8) construct and interpret structural equation models to estimate the direct and indirect effects of quantitative and qualitative traits on grain yield per plant for each landrace population. The results will be discussed within the context of on-farm conservation and sustainable utilization of endangered wheat landrace populations under subsistence farming and to illustrate the use of advanced multivariate statistical methods in assessing phenotypic variation in sub-divided landrace populations.

Key words: Genetic Diversity, Landrace, Oman, Phenotyping, Wheat

Introduction

Oman and the rest of the Arabian Peninsula have an ancient history of crop cultivation of indigenous as well as exotic plant species (Guarino, 1990; Hammer et al., 2004), including bread, durum, and other minor wheat species (Al-Maskri et al., 2003). However, little is known about the wealth of plant genetic resources in Oman due to a multitude of anthropogenic, physiographic and historic reasons. In particular, little is known about Omani indigenous wheat landraces as to their morphological variation, genetic structure, agronomic properties, and tolerance to biotic and abiotic stress, especially high temperature and salinity (Ahmad et al., 2013), and quality characteristics. Due to the aridity of its climate, irrigation is necessary for crop growth in all of Oman except for the southernmost parts of the country, which receive summer monsoon rains; therefore, it is speculated that a certain level of genetic diversity for salt tolerance may exist in wheat landraces from Oman (Jaradat et al., 2004).

Various definitions of a land race have evolved since the end of the 19th century. Owing to their complex nature, Zeven (1998) concluded that an all-embracing definition cannot be given. A working definition: "a land race is a dynamic population(s) of a cultivated plant that has historical origin, distinct identity and lacks formal crop improvement, as well as often being genetically diverse, locally adapted and associated with traditional farming systems." Nevertheless, Harlan (1992) defined a landrace as a mixture of genotypes that evolved, largely by natural selection, under environmental conditions in which they were grown. In wheat, as a self-pollinated crop, the genotypes of the mixture are mostly homozygous. A wheat landrace being composed of a mixture of homozygous genotypes usually exhibits considerable genetic variation for developmental (i.e., phenological traits), qualitative and quantitative traits (Camacho-Villa et al., 2005; Al-Khanjari et al., 2008; Jaradat, 2013).

Wheat landraces comprise the major genetic resource of cultivated wheat in many developing countries in the Middle East and North Africa (Belay et al., 1995; Jaradat, 2006; Ahmadizadeh et al., 2011), including Oman (Al-Maskri et al., 2003Al-Khanjari et al., 2007; Filatenko et al., 2010; Filatenko and Hammer, 2014). During the last ~30 years of the 20th century, an international campaign resulted in collecting and conserving these landraces in genebanks; their vernacular names and some of their characteristics have been documented (Guarino, 1990; Brush and Meng, 1998). As distinct plant populations, landraces are named and maintained by traditional farmers to meet their social, economic, cultural, and environmental needs. They are alternately called farmers' varieties or folk varieties (Belay et al., 1995; Masood et al., 2005; Karagöz and Zençirci, 2005; Zençirci and Karagöz, 2005) to indicate the innovative role of farmer communities in their development and maintenance. A wheat landrace is not necessarily a genetically and phenotypically stable, distinct, and uniform unit. Its diversity is linked to the diversity of the material sown in its immediate geographical vicinity, and to the level and frequency of short- and long-distance seed exchange among farmers (Almekinders et al., 1994; Brush and Meng, 1998).

Wheat may have been introduced into Oman and other parts of the Arabian Peninsula through trade with ancient cultures of Mesopotamia (Gebauer et al. 2010). Though time of wheat introduction into Oman is not certain, it has been cultivated in various oases of the country for about 3,000 years (Guarino, 1990; Al Maskri et al., 2003; Gebauer et al., 2010). Subsequent to its introduction, both bread and durum wheat germplasm was subjected to evolutionary modifications as a result of natural selection and adaptation (Ali Deb et al., 1992) to the harsh desert environment prevailing in the region, and especially to the agroecological conditions of mountain and desert oases of Oman (Filatenko et al., 2010; Gebauer et al., 2010; Filatenko and Hammer, 2014). Several collecting expeditions by local (Al-Maskri et al., 2003; Al-Khanjari et al., 2008) and international (Guarino, 1990) gene hunters succeeded in collecting indigenous wheat and barley (Jaradat et al., 2004) landraces, and identified rare species being conserved *in situ* in mountain oases. Omani wheat landraces (*Triticum* spp.) which show broad spectrum of diversity (Al Maskri et al., 2003; Al Khanjri et al., 2005; Zhang et al., 2006) represent, at least, five species, including *Triticum aestivum, T. durum* (Guarino, 1990) *T. dicoccon* (Hammer et al., 2004), *T.*

aethiopicum (Al Khanjri et al., 2008) and *T. compactum* (Filatenko et al., 2010). These species represented hexaploid (*T. aestivum* and *T. compactum*) and tetraploid (*T. dicoccon, T. aethiopicum* and *T. compactum*) wheats. Most studies carried out on Omani crop landraces, including wheat and barley, concluded that a large and valuable diversity was available in the country and attributed this large diversity, in part, to the geographic location of the country, its physiography, as well as to germplasm exchange with its ancient trading partners in the Far East, South Asia, East Africa, especially Ethiopia through Yemen, and the larger Middle East (Harlan, 1992; Zohary and Hopf, 2000; Gebauer et al., 2010). Farmers in Oman, typical of subsistence and resource-poor farmers in wheat marginal growing regions, usually grow a mixture of locally-adapted wheat species, including tetraploid and hexaploid landraces (Zhang et al., 2006; Al Khanjri et al., 2007); these mixtures occasionally result in hybrid swarms (Mastuoka, 2011) thus generating new diversity and contributing to yield buffering and stability under adverse environmental and management conditions (Al Khanjari et al., 2008). In addition, it is suggested (Zeven, 2000; Tesgaye and Berg, 2007; Karagöz and Zençirci, 2005; Yedliay et al., 2011) that farmers grow and maintain highly variable wheat landraces to lower the risk of failure under marginal production conditions and to increase food security of isolated communities (Rijal, 2010).

Wheat landraces are genetically heterogenous populations comprising inbreeding lines, and hybrid segregates generated by the low level of random outcrossing during hundreds, if not thousands, of generations (Harlan, 1992; Camacho-Villa et al., 2005). Having evolved over many generations in a multitude of environments and local farming systems, wheat landraces have developed abundant patterns of variation and would represent a largely untapped reservoir of useful traits for adaptation to biotic and abiotic stresses (Ali Deb et al., 1992). Throughout their evolutionary history, wheat landraces have been shaped and molded mainly by farmers to meet diverse end uses (Zeven, 2000), cultural practices, and to respond to changing socio-economic and growing conditions (Brush and Meng, 1998; DeLacy et al., 2000; Jaradat, 2006).The development of new varieties from landrace populations is a viable strategy to improve landrace yield and yield stability, especially under stress and to combat future climate change (Moghaddam et al., 1997; Zaefyzadeh et al., 2009; Jaradat, 2013).

Diversity of wheat landrace populations, when structured to build spatial and temporal heterogeneity into cropping systems will enhance resilience to climate change and the abiotic and biotic stresses associated with it. Other resilience sources will include more robust genetic resistances and biochemical response mechanisms derived from unique landrace genotypes (Bonman et al., 2007). These effects will be difficult to dissect and model as their mechanistic bases are generally not well-understood. The manner with which wheat landraces and their populations in and outside their centers of diversity, especially in marginal areas such like Oman, might respond to climate change will determine their continued productivity, utility, and survival (Gebauer et al., 2010; Ribeiro-Carvalho et al., 2004; Jaradat et al., 2004). Wheat plants will probably respond to climate change through shifts in morphology (e.g., tillering capacity, leaf area index, green leaf area duration), phenology (e.g., days to anthesis, days to maturity, duration of seed filling period), or development (e.g., rate of leaf emergence based on available growing degree days), which may help maintain fitness. However, phenotypic plasticity and gene flow (mainly through seed exchange and occasional outcrossing) of landraces may not produce fully adapted phenotypes or the necessary genetic variation to combat climate change (Almekinders et al., 1994; Ribeiro-Carvalho et al., 2004; Moragues et al., 2006).

The mountain and desert oases, which comprise traditional repositories and natural evolutionary laboratories of landraces of wheat and other valuable crops in Oman, are being urbanized (Gebauer et al., 2010); and their plant genetic resources, including those of wheat, are being threatened with genetic erosion. Due to the introduction of high-yielding varieties and adoption of alternative cash crops, farmers are increasingly abandoning their traditional landraces and cultivating new varieties. Although wheat was never a major crop in Oman due to several physiographic and socio-economic factors (Zhang et al., 2006), its cultivation continued, especially in scattered oases around the country for the last ~3,000 years and resulted in a wealth of genetic diversity that can be of value to the Omani farmers and for use by national, regional and international wheat breeding and improvement programs.

It was estimated that the land area under wheat landraces in Oman decreased by 75% in a span of 8 years (Al Khanjari et al., 2008). A total of 1,000 ha of land were under wheat cultivation in the 1960s and produced 1,400 tons of grain; however, in 2011, wheat was cultivated on about 640 hectares and produced about 2,100 tons of grain (FAO, 2011); these production figures may reflect replacement of landraces with high yielding wheat varieties and the adoption of improved management practices. Although farmers may have several socio-economic incentives to replace wheat landraces with high-yielding introduced varieties, several landraces are still being cultivated by subsistence farmers in Oman; presumably due to their high adaptability, tolerance to salinity in the desert oases, and perhaps due to the quality of their products. The objectives of this study were to: (1) identify and construct multivariate distances between landrace populations, (2) identify plant- and seed-related traits contributing to its composition, (3) build principal components that can account for maximum variation, (4) quantify variance components accounted for by major seed qualitative traits, (5) partition total diversity and estimate levels of population differentiation, (6) build a predictive model of the association between landrace population-trait and a number of plant-, spike-, and seed-based traits, (7) identify traits affecting spikelet fertility as a critical component of grain yield under the prevailing hot conditions in Oman, and (8) construct and interpret structural equation models to estimate the direct and indirect effects of phenological, quantitative and qualitative traits on grain yield per plant for each landrace population.

Materials and Methods
Wheat landrace germplasm

In 2003, a bulk sample of wheat seed was obtained from a farmers' market of Buraimi, Dhahira, Oman and was planted during winter of 2003-04 at the Experiment Station of the International Center for Biosaline Agriculture (ICBA), Dubai (25°13 N and 55°17 E) for seed multiplication, to identify components of the landrace, and to select maximum diversity within the seed sample for a follow-up study. Regular management practices for wheat management under irrigation were followed. Plant phenology was documents as to days to heading, filling period and days to maturity. At maturity single plant selections were made on the bases of spike and plant morphological characteristics. Five populations were identified within the landrace on the basis of preliminary phenotypic evaluation, and five sub-samples, each of 160 plants, were selected for the follow-up characterization and evaluation. Ten

spikes per sub-sample were used for spike and seed characterization.

Characterization of the germplasm

Selected plants were characterized as to qualitative (awn color, awndness, brush size, germ size, glume color, glume pubescence (or hairiness), seed color, seed shape, spike diversity and vitreousness) and quantitative (plant height, spike length, awn length, 100- seed weight or kernel weight, spikelets per spike, seeds per spike, seed length and seed width). Wheat descriptors (IBPGR, 1995) were slightly modified to fit the objectives of this study as follows: Spike density 1= very lax, 9 = very dense (and a quantitative measure of spike density was developed based on number of spikelet groups per unit spike length); Awndness: 0 awnless, 3 awnletted, 7 awned; Awn/glume color: 0 white, 1 creamy, 2 red-brown, 3 purple-black; Glume pubescence: 0 absent, 3 low, 7 high; Seed color: 0 white, 1 slight red, 2 red, 3 purple; Seed vitreousness: 3 soft, 5 partly vitreous, 7 vitreous, and Germ size: 1 small, 2 medium, and 3 large. The ratio of awn length to spike length and spike length to plant height were calculated for each plant; then the spikelet fertility was estimated as the number of seed per spikelet.

Statistical analyses

We used several dependence and interdependence statistical analyses methods and models to perform the multivariate analyses of the phenological, quantitative and qualitative data measured on single plants from five populations in a wheat landrace from Oman. Basic statistics were developed for the whole landrace, each population and each sub-sample. Mean separation for phenological and quantitative traits was carried out using a multiple range test after the analysis of variance was performed and a coefficient of variation was estimated for each entry. Grain yield per plant was adjusted to 155 g kg^{-1} grain moisture at harvest for each landrace population. In order to satisfy assumptions of uni- and multivariate analyses of variance, all variables were subjected to the Leavene test of homogeneity of variances and to the Shapiro-Wilk W test for normality (StatSoft Inc., 2012), then the appropriate data transformation was carried out (Zar, 1996); transformed data was back transformed for reporting.

Canonical discriminant analysis was used to determine which variables discriminate between the five landrace populations and to estimate the standardized discriminant coefficient for the first two canonical discriminant roots for each significant variable entered in the canonical

discriminant analyses. In addition, the eigenvalues, cumulative proportion of variance explained by the first two canonical roots, and percent correct classification of landrace populations were estimated. Pairwise distances between landrace populations were estimated based on all phenological, quantitative and qualitative traits. Components of the non-linear iterative partial least squares (NIPALS) were used for each landrace population in the diagnostics and dimensionality reduction with the objective of representing the set of multivariate variables with the aid of one principal component. A linear mixed model was used to estimate variance components and modeling of covariance structures using the method of residual maximum likelihood (REML). Landrace populations were used as a fixed factor to perform a regular analysis of variance, while the qualitative variants each of glume pubescence, spike density, spike awndness, awn/glume color, seed color, and seed vitreousness, was used as a random factor to estimate the variance accounted for by these descriptors within the whole landrace.

The frequency of qualitative descriptors, in addition to those developed from phenological and quantitative traits (see below) were used to estimate the Shannon-Weaver Information Index (H') and to estimate total diversity and the population differentiation in the whole landrace and in each of its populations. The least square means and standard deviation calculated for each of the phenological and quantitative traits and landrace were used to categorize each trait into three discrete groups [i.e., (small)<= mean - 1.0 SD., (medium) > mean-1.0 SD< mean + 1.0 SD., and (Large) >= mean + 1.0 SD] according to Zar (1996). A polymorphic diversity index (Zhang and Allard, 1986) was calculated for each land race population and trait based on the relative phenotypic frequencies for each categorical trait as:

$$H' = -\Sigma\ pi \ln pi \text{ for } i = 1, 2, ..n.$$

Where pi is the relative frequency ith category of the jth trait and was used as a measure of phenotypic diversity.

Total genetic diversity (H_T), and its components were calculated for each land race population using frequencies of all categorical traits, then a population differentiation coefficient (proportion of total genetic diversity found within populations, G_{ST}) was calculated according to Hamrick and Godt (1989) using the software program PopGene v. 3.2. (Yeh et al., 2000). The sequential and joint hierarchical nested cluster analyses were employed to cluster subpopulations and traits based on

standardized data. Structural equation modeling was employed to identify direct and indirect effects of quantitative and qualitative traits and groups of traits on grain yield per plant for each population within the landrace. For each landrace population, two structural equation models were developed; one was based on quantitative traits and the other on qualitative traits. The validity of each model was tested using a χ^2 test. All statistical analyses were carried out using relevant modules in STATISTICA v. 10 (StatSoft Inc., 2012) and PopGene v. 3.2. (Yeh et al., 2000).

Results
Univariate Analyses of Variance
The least square means and mean separation results (Table 1) indicated that there were pairwise significant differences ranging from 2 to 5 landrace populations (i.e., between a minimum of 2 and a maximum of all 5 LR populations). There were no significant differences between landrace populations for most seed traits (e.g., seed width, seed length and 100-seed weight); however, there were minor differences for filling period, and spike/plant ratio; and large differences for most of the remaining traits, especially spike fertility where each landrace population differed significantly from the others. Means of spikelet fertility ranged from a minimum of 2.003 (LR1) to a maximum of 3.399 (LR5). Two of the LR populations can be considered as semi-dwarf with a mean plant height of 67 (LR1) and 69 cm (LR2). These LR population had the largest spike length/plant height ratio but

the smallest spikelet fertility; however, with significant differences for most traits, especially phenological traits. LR5, with the highest spikelet fertility is characterized by the tallest plants and differed significantly from other LRs for the majority of measured and estimated phenological traits. The remaining LRs (LR3 and LR4 were mostly intermediate between LR1 and LR5 populations.

Canonical Discriminant Analyses
A two-dimensional plot (Figure 1) was developed on the basis of significant multivariate differences between and within LR populations. The first canonical discriminant root accounted for 72% of total variation in the whole germplasm collection and resulted in separating LR population on the basis of the among-LR differences; whereas, the second discriminant function accounted for 18% of the variation and reflected variation within LR populations. Based on the classification models developed for each LR population (data not presented), the average correct classification was 87% and ranged from 91% correct classification of LR3 to 79% of LR5 population. Several traits contributed to this level of correct classification with negative and positive loadings on both discriminant functions (Table 3). The largest miss-classification, and the overlap between LR populations, was found between LR3 and LR4; whereas, 21% of entries in LR5 were miss-classified as belonging to LR3.

Table 1. Least square means and mean separation between five populations (LR1 to LR5) for phenological and quantitative traits measured on 800 plants of a wheat landrace from Oman.

Trait	Least squares means				
	LR1	LR2	LR3	LR4	LR5
Plant height, cm	66.98d§	69.43d	86.79c	91.35b	101.45a
Spike length, cm	10.24b	11.92ab	9.62b	9.46b	13.43a
Awn length, cm	3.42c	4.69b	2.44d	2.24d	6.15a
Spikelets/spike	16.83b	17.54b	22.51a	20.74a	23.98a
Seeds/spike	33.82d	46.97c	67.54b	47.83c	81.22a
Spike density	3.715c	4.479b	8.215a	5.839b	7.395a
Seed length, mm	6.51a	6.16a	6.31a	6.33a	3.27b
Seed width, mm	2.796	2.945	2.965	2.903	2.977
Seed size, mm^{-3}	2.359	2.114	2.162	2.217	2.146
100-seed wt, mg	3.2223	3.2789	3.2013	3.3412	3.4539
Days to heading	100.06a	82.33c	92.13b	93.34b	89.83b
Days to maturity	133.6a	125.8c	128.53b	128.98b	126.22c
Filling period, days	33.57c	43.51a	36.39b	35.62b	36.39b
Spike/Plant length	0.156a	0.174a	0.111b	0.104b	0.132ab
Awn/Spike length	0.2687b	0.346a	0.1672c	0.1586c	0.3541a
Spikelet fertility	2.033e	2.72c	3.035b	2.341d	3.399a

§, Least squares means within each row followed by the same letter do not differ significantly using Duncan Multiple Range Test (p<0.05).
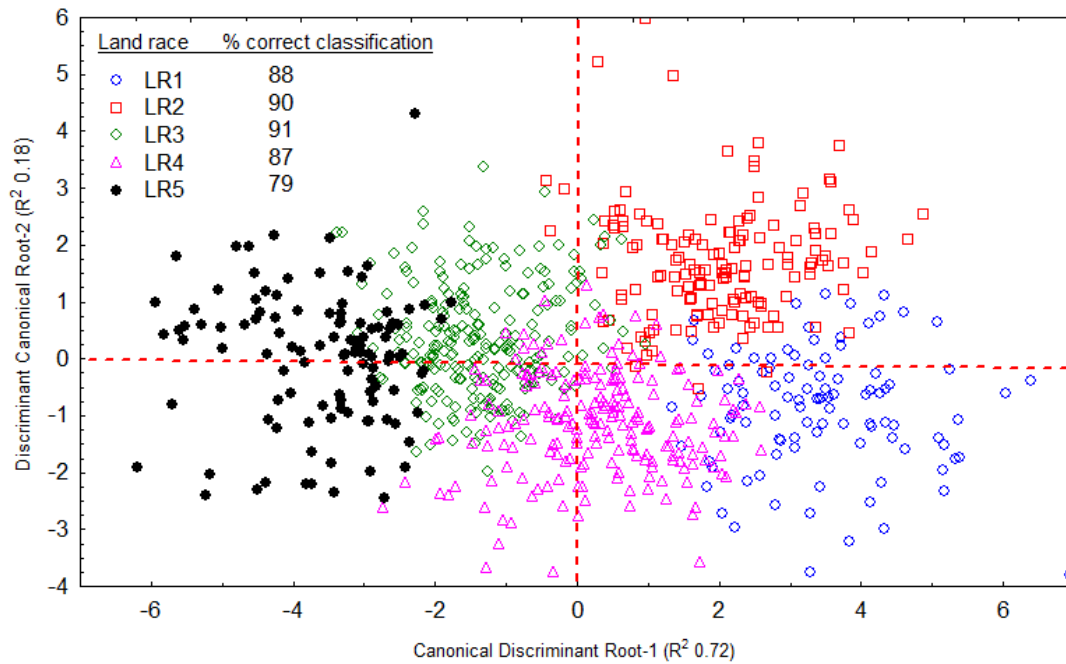
Figure 1. Canonical Disctriminant analyses between five populations (LR1 to LR5) and percent correct classification of these landrace populations based on phenological, quantitative and qualitative traits in a wheat landrace from Oman. (See Table 2 for details)

Most traits contributed to the large (79-91%) correct classification between LR populations; however, only two phenological traits (days to maturity and filling period), two ratios (spike length/plant height and awn length/spike length) and spikelet fertility had no significant F-values due to large within LR population variation as compared to among LR population variation. However, all of these traits had sizable negative or positive loadings on both discriminant functions except filling period (Table 2). Three quantitative traits (seed width, seed size and kernel weight) and one qualitative trait (awndness) had non-significant F-values; while the majority of traits that contributed to the multivariate discrimination between LR populations had significant F-values and had large (>50) coefficients of determination (R^2 values) except days to anthesis and seed length (R^2=0.38), and seed color (R^2=0.36), seed brush (R^2=0.45) and vitreousness (R^2=0.37).

Trait associations and loadings (positive or negative standardized coefficients; Table 2) on each canonical discriminant function indicated a complex picture when all five LR populations were considered. Of the 17 traits with loadings on both discriminant functions, only four had positive and four had negative loadings on both functions. Eight traits (four quantitative and four qualitative) had positive loadings on the first canonical function and

the remaining nine traits had negative loadings (seven quantitative and two qualitative traits) on the same discriminant function which accounted for 72% of total variation and contributed to discrimination between LR populations. Trait associations and loadings on the second canonical discriminant function, as indicated previously, accounted for the remaining 18% of total variation, and contributed to the within LR population discrimination. Nine traits (six quantitative and three qualitative traits) had positive loadings, and eight traits (five quantitative and three qualitative traits) had negative loadings on the second discriminant function. Groups of associated traits can be identified from Table 3 and their power of discrimination can be inferred from the values of their standardized coefficients and the R^2 values associated with their p-values. For example, the following traits with standardized coefficients on the first canonical discriminant function are the most to discriminate between the five LR population; these were: plant height (standardized coeficient of -0.815), seed length (-0.77), and awn/glume color (-0.67). On the other hand, plant height and awn length with standardized coefficients of -0.536 and -0.971 on the second canonical discriminant function, were the most to contribute to the within-LR population discrimination.

Table 2. Summary statistics and tests of significant for canonical discriminant analyses between five populations of wheat landrace from Oman based on phonological, quantitative and qualitative traits measured or scored on 800 single plants.

Traits	Wilks' λ	F-remove	p-value	R^2	Standardized coefficients	
					CDR1(R^2=0.72)	CDR2 (R^2=0.18)
Quantitative						
Plant height	0.053	34.8	0.0001	0.73	-0.815	-0.536
Spike length	0.047	7.3	0.0008	0.98	-0.188	1.309
Awn length	0.047	6.5	0.0003	0.98	0.279	-0.971
Spikelets/spike	0.052	27.3	0.0001	0.91	-0.079	0.404
Seeds/spike	0.057	49.1	0.0001	0.93		
Spike density	0.049	15.1	0.0001	0.93	0.071	1.185
Seed length	0.046	2.9	0.0186	0.38	-0.770	-0.009
Seed width	0.046	0.9	0.4812	0.26		
Seed size	0.045	0.7	0.5754	0.53		
Kernel weight	0.045	0.7	0.6152	0.51		
Days to anthesis	0.055	39.1	0.0001	0.38	0.113	-0.545
Days to maturity					-0.051	-0.183
Filling period						
SpikeL/Plht					0.113	0.049
AwnL/SpikeL					-0.292	0.556
Spikelet fertility					-0.006	0.566
Qualitative						
Awn/glume color	0.047	3.7	0.005	0.64	-0.670	-0.050
Awndness	0.046	2.1	0.085	0.89	0.330	0.081
Seed color	0.048	4.0	0.004	0.36	0.151	0.136
Seed brush	0.045	2.9	0.021	0.45	0.089	-0.086
Glume hair	0.048	3.7	0.005	0.63	0.135	-0.171
Vitreousness	0.050	3.8	0.021	0.37	-0.018	0.179

Table 3. Mahalanobis distances based on 24 phenological, quantitative and qualitative traits and level of significance between five populations of a wheat landraces from Oman. (See Figure 1)

LR population	Squared Mahalanobis Distances between LRS (above diagonal) and F-value (below diagonal ($p(F)$<0.05 for all F-values)				
	LR1	LR2	LR3	LR4	LR5
LR1		11.6	26.3	14.4	51.9
LR2	35.8		14.7	11.4	8.2
LR3	96.1	68.4		6.7	8.2
LR4	50.2	50.1	37.6		19.1
LR5	142.4	115.7	31.9	70.8	

The results of dsicriminant analyses also provided an indirect indication of which quantitative and qualitative traits are likely to be associated at the whole LR level. The association on the first canonical discriminant function of plant height, spike length and seed length, as quantitative traits, with awn/glume color, as qualitative trait, is an interesting example. Another interesting disassociation between awn/glume color (with a standardized coefficient of -0.67) and awndness (with a standardized coefficient of 0.33) on the first

canonical discriminant function suggested that these traits contributed in opposite direction at the whole LR level and that certain awn/glume colors are associated or disassociated with certain phenotypes of awndness (awnless, awnletted, and awned).

Multivariate Distances between LR Populations
Multivariate distances between centroids of LR populations were obtained from the results of the canonical discriminant analyses. These distances (Table 3) are indicative of how close or far these

LR populations are from each other based on the cumulative significant differences among traits. The multivariate distances between LR populations, were expressed as Squared Mahalanobis Distances (SMD) and ranged from 6.7 between LR3 and LR4 to a maximum of 51.9 between LR1 and LR5 (Table 3). The largest distance was almost twice as large as the next largest distance (26.3) between LR1 and LR3 and seven times as large as the smallest distance. All SMDs were significantly different as indicated by the F-values.

Trait Association at the LR population Level

Results of the principal components analyses for each LR population are presented in Figures 2 to 6, and will be discussed separately for each LR population due to some similarities and sizeable differences in the results of these analyses. We present results associated with the first principal component, as it accounted for the maximum variation, at the calibration (R^2) and validation (Q^2) phases of principal components model building in all phenological, quantitative and qualitative traits for each LR population. Additionally, we point to those traits with high loadings (i.e., correlation coefficient with the first principal component having *r*-values above or below 0.5) as they are the ones which may differentiate one LR population from another population with large and significant probability.

The first principal component accounted for 32 and 21% of total variation in LR1 population at the

calibration and validation stages of model building (Figure 2). The validation phase captured 65% of the amount of variation accounted for by the calibration phase, which is an indication of how reliable the model can be, regardless of the calibration coefficient of variation. Most traits had loadings within the ±0.5 boundaries around zero, including phenological traits. Both of days to heading and days to maturity had opposite loadings to that of filling period, which suggests that the length of grain filling is negatively associated with the length of the vegetative growth phase. The spike length and awn length were associated with the awned phenotype (7 on the descriptor list) and with colored awns and colored seed were the most important qualitative traits with positive loadings on the first principal component.

Alternatively, kernel weight was associated with vitreous kernels and both had negative loadings along with awnless spikes and white- or cream-colored seed. Finally, a few traits had close to zero loadings and did not contribute substantially to the variation explained by this principal component; these include, for example, days to maturity, seed length, and spikelets per spike. The disassociation between spikelet fertility and kernel weight, and their association with less vitreous and highly vitreous kernels, respectively, are examples of quantitative/qualitative trait relationships that can be of value in germplasm collection, characterization or selection.
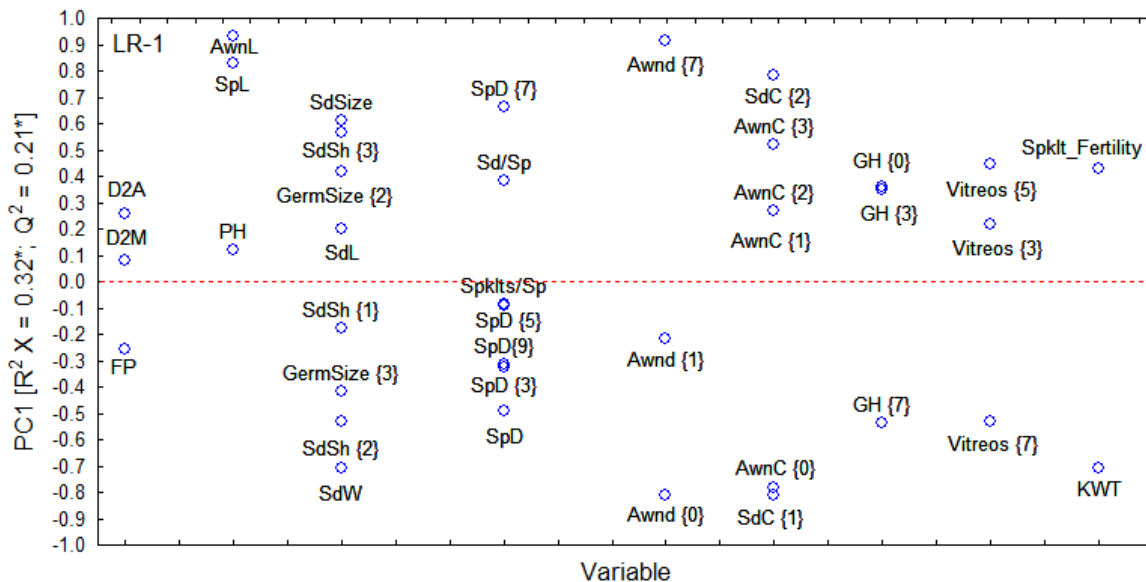

Figure 2. The first principal component (PC1) and coefficients of determination at the prediction (R2) and validation (Q2) phases of PC model building derived from phenological, quantitative and qualitative traits in the first population (LR1) in a wheat landrace from Oman.

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The second LR population (LR2), which is separated by 11.6 SMD units from LR1 (Table 3) displayed a different picture of trait association on the first principal component, which explained 32 and 16% of total variation at the calibration and validation phases of model building, respectively (Fig. 3). The validation phase captured only 50% of the amount of variation accounted for by the model at the calibration phase. Plant height, in addition to phenotypic variants of a few qualitative traits, had close to zero loadings on the first principal component. Traits with the largest positive loading were spike density (qualitative and quantitative) which were associated with the awnless and purple spike colored phenotypic variants; whereas, long awns and long spikes, along with white colored awn phenotypic variant, had negative loadings on the principal component. Kernel weight (as well as plant height and filling period, as mentioned earlier) had small positive loadings and were negatively associated with spikelet fertility, in a sharp contrast with LR1.

The third LR population was closer to LR2 (SMD=14.7) as compared to its distance from LR1 (SMD=26.3), and presented, yet, another unique set of trait loadings and associations. The first principal

component explained 28 and 17% of total variation at the calibration and validation phases of model building, respectively (Figure 4). The validation phase captured 61% of the amount of variation accounted for by the calibration phase. Very few trait variants had loading above or below the 0.5 boundaries in this LR. The small Q^2 value of 17% is an indication of this characteristic in LR3.

Relationships between phenological traits differed in this LR population from the previous populations by having positive loadings of, and association between, filling period and days to maturity; both of which were at the opposite side of days to heading; however, all three traits had loadings within the ±0.5 boundaries around zero, with spike fertility being associated with filling period, while kernel weight was associated with days to heading (Figure 4). Notably, spike length and awn length, naturally being associated with each other in the awned phenotypes, they had the largest positive loadings and were not associated with plant height which did not contribute to the explained variation in LR3 population. On the other hand, seed and awn color associations were similar in magnitude to those in LR1, but not in LR2 population.

Figure 3. The first principal component (PC1) and coefficients of determination at the prediction (R2) and validation (Q2) phases of the PC model building derived from phenological, quantitative and qualitative traits in the first population (LR2) in a wheat landrace from Oman.
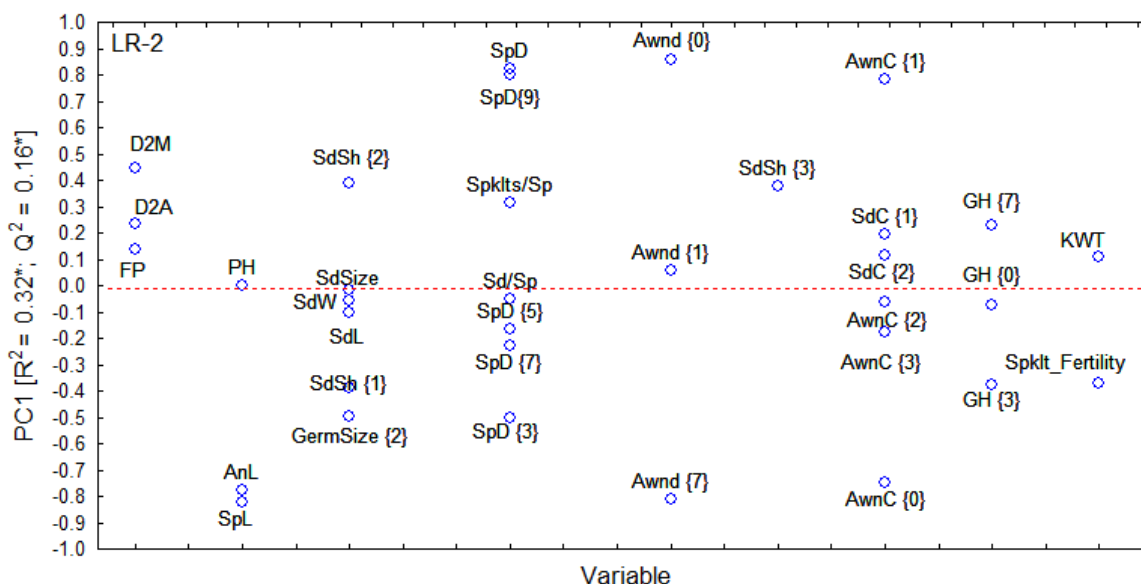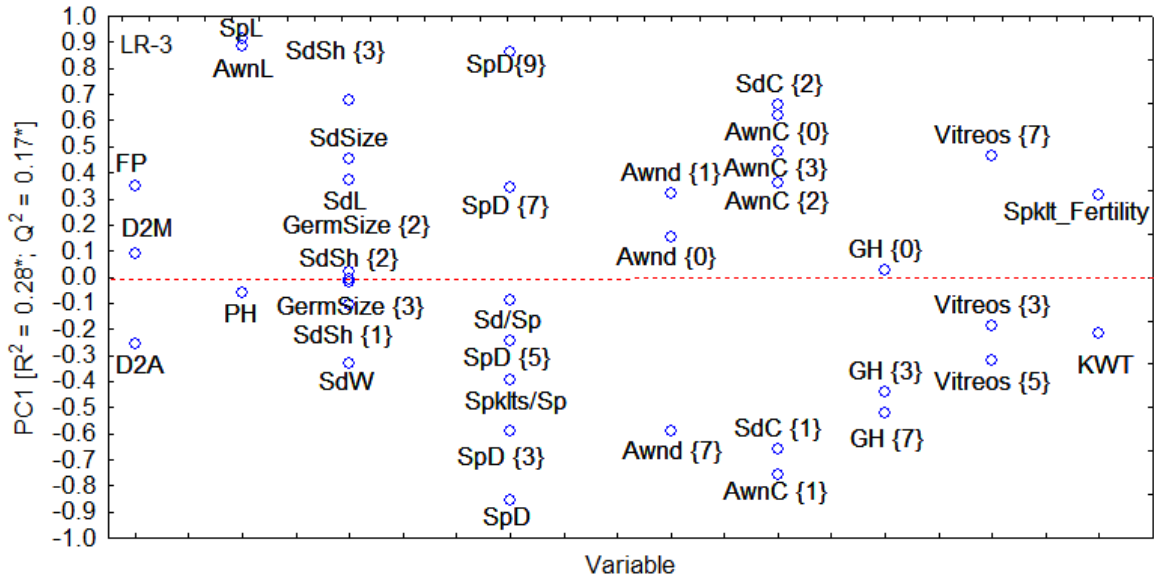
Figure 4. The first principal component (PC1) and coefficients of determination at the prediction (R2) and validation (Q2) phases of the PC model building derived from phenological, quantitative and qualitative traits in the first population (LR3) in a wheat landrace from Oman.

The LR4 population was closest to LR3 (SMD=6.7) and was at slightly larger distance from LR1 (SMD=14.4) than LR2 (SMD=11.4) (Table 3); it displayed a totally different pattern of trait loadings and associations on the first principal component, which accounted for 33 and 22% of total variation at the calibration and validation phases of model building (Figure 5). The validation phase captured 67% of the amount of variation accounted for by the calibration phase. Tight association between phenological traits, at the one hand, and between spikelet fertility and kernel weight, on the other, characterized LR4. The phenological traits had almost zero loadings, whereas, spikelet fertility and kernel weight had positive loadings on the first principal component. About 13 variants of qualitative and quantitative traits had large, positive or negative loadings, and displayed some unique associations as can be seen in Figure 5. Finally, LR5 was separated by the largest distance from LR1 (SMD=51.9), intermediate distance from LR4 (SMD=19.1) and
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smallest and equal distances from LR2 and LR3 (SMD=8.2) (Table 3). The first principal component explained 32 and 16% of total variation at the calibration and validation phases of model building (Figure 6). The validation phase captured the smallest (50%) amount of variation accounted for by the calibration phase, as compared to other LR populations. Trait loadings on the first principal component and association of different variants LR5 population were almost mirror-image (and in some cases, similar to) of loadings displayed by LR3 population (which was the closest in SMD measure to LR5). Filling period had a zero loading and was closer to days to heading than days to maturity in LR5, which was observed in LR3 population. Plant height was disassociated from spike and awn length; the latter had large and positive loadings on the first principal component, a mirror image of their loadings in LR3 population. The same analogy can be made about awn and seed colors, on the one hand, and spikelet fertility and kernel weight, on the other.
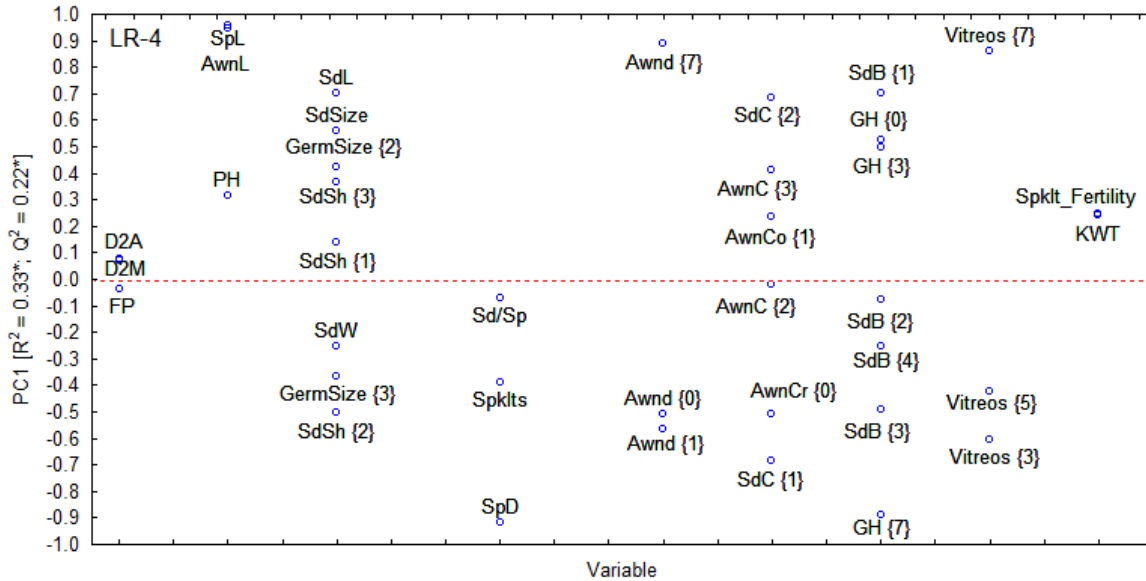
Figure 5. The first principal component (PC1) and coefficients of determination at the prediction (R2) and validation (Q2) phases of the PC model building derived from phenological, quantitative and qualitative traits in the first population (LR4) in a wheat landrace from Oman.
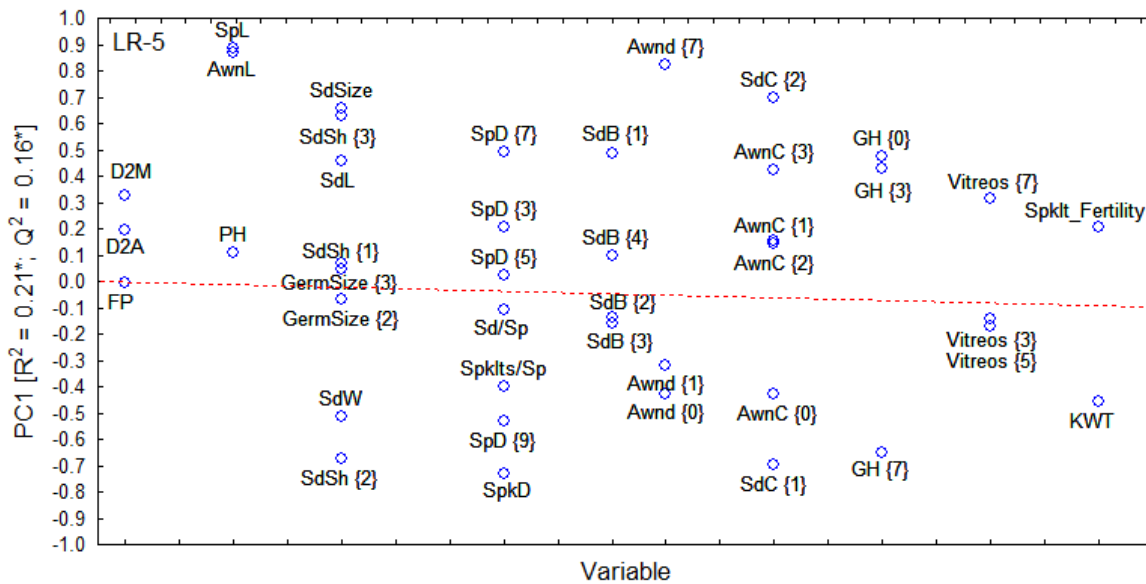
Figure 6. The first principal component (PC1) and coefficients of determination at the prediction (R2) and validation (Q2) phases of the PC model building derived from phenological, quantitative and qualitative traits in the first population (LR5) in a wheat landrace from Oman.

Variance Components Analyses

Results of the mixed linear models used to estimate fixed and random effects on phenotypic and quantitative traits are presented in Tables 4 to 9. Variants of six qualitative traits within LR populations (glume pubescence, spike density, spike awndness, awn color, seed color, and seed vitreousness) were used as random factors, whereas, in each case, the LR populations were used as a fixed factor. The level of significance for the fixed factor was reported as the probability of an *F*-value, and the percent variance explained by the random factor(s) and the level of significance were reported using the probability of a *z*-value.

Significant differences between LR populations were found for only six of the 16 traits in this

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analysis (Table 4). The most significant differences were found for plant height, spikelets per spike, seeds per spike, days to heading and spikelet fertility. The F-values (and their level of significance) can be used to compare among- to within-LR levels of variation in these traits. Variance components analysis using glume pubescence as a random factor (Table 4) resulted in a wide range of variances (5.1% for seed width to 71.7% for spike length) being explained by this phenotypic descriptor. However, if we consider 50% as a cutoff for a reasonably satisfactory level of variance being explained by the random factor, then the variances in only six of the 16 quantitative traits can be considered as acceptable. However, the explained variances in only two traits (seeds/spike and seed width) were not significant. Groups of traits can be identified based on their phenotypic associations as having large (spike length, awn length, spikelets per spike, and spike density), medium (phenological traits) or a small (plant height and spikelet fertility) portion of their variation being explained by the random factor.

Table 4. Variance analyses (using landraces as fixed factor) and variance components analyses (using <u>glume hairiness</u> variants as random factor) of phenological and quantitative variables in a wheat landrace from Oman.

Variable	Fixed factor		Random factor		
	F-value	*p-F*	% variance	*z*-value	*p-z*
Plant height	39.10	0.0001	18.3	1.74	0.042
Spike length	0.18	0.94	71.7	2.19	0.014
Awn length	0.22	0.91	69.2	2.18	0.014
Spikelets/spike	9.01	0.002	25.2	1.85	0.032
Seeds/spike	91.80	0.0001	8.9	1.37	0.084
Spike density	1.18	0.41	65.6	2.25	0.015
Seed length	0.19	0.93	49.9	2.15	0.017
Seed width	2.37	0.122	5.1	1.36	0.092
Seed size	0.63	0.65	29.9	1.96	0.025
Kernel weight	1.53	0.26	25.1	2.01	0.022
Days to heading	6.27	0.008	31.1	1.99	0.023
Days to maturity	2.22	0.14	34.8	2.03	0.021
Filling period	5.11	0.016	25.6	1.86	0.031
Spike/Plant height	1.08	0.41	58.4	2.16	0.015
Awn/Spike length	0.19	0.94	60.4	2.18	0.014
Spikelet fertility	13.20	0.005	17.7	1.85	0.032

Table 5. Variance analyses (using landraces as fixed factor) and variance components analyses (using spike density variants as random factor) of phenological and quantitative variables in a wheat landrace from Oman.

Variable	Fixed factor		Random factor		
	F-value	*p-F*	% variance	*z*-value	*p-z*
Plant height	80.30	0.0001	9.2	1.75	0.039
Spike length	1.28	0.32	33.2	2.35	0.009
Awn length	1.11	0.39	34.9	2.24	0.012
Spikelets/spike	6.12	0.005	39.5	2.38	0.008
Seeds/spike	83.90	0.0001	11.9	1.81	0.034
Spike density	2.46	0.09	30.5	2.37	0.009
Seed length	0.77	0.55	24.4	2.16	0.015
Seed width	0.66	0.67	14.3	2.04	0.020
Seed size	0.96	0.46	16.3	2.05	0.020
Kernel weight	0.51	0.72	27.9	2.24	0.012
Days to heading	8.33	0.001	26.5	2.20	0.013
Days to maturity	8.00	0.028	16.6	2.08	0.018
Filling period	4.37	0.02	28.5	2.25	0.012
Spike/Plant height	2.40	0.11	32.7	2.37	0.009
Awn/Spike length	0.83	0.52	36.1	2.30	0.010
Spikelet fertility	30.70	0.0001	10.7	2.03	0.021

Seven quantitative traits expressed significant differences, and one trait was marginally significant, in the analysis of variance when spike density was used as a random factor (Table 5). Almost the same traits identified in Table 4 had the same or similar levels of significance as in Table 5; however, the levels of significance, as measured by *F*-values and the among- to within-LR variances were different. Spike density (as a categorical trait) was a much stronger factor than glume pubescence in accounting for variances in all quantitative traits

(Table 5); however, none of the explained variances reached the 50% level. The range in the amount of variances was much smaller (9.2% for plant height to 39.5% for seeds per spike) as compared to those for glume pubescence (Table 4). Most traits (10 traits) had >20% of their variances accounted for by the random factor; whereas, the remaining six (plant height, seeds per spike, seed width and size, days to maturity, and spikelet fertility) had <20% of their variances explained.

Table 6. Variance analyses (using landraces as fixed factor) and variance components analyses (using spike awndness variants as random factor) of phenological and quantitative variables in a wheat landrace from Oman.

Variable	Fixed factor		Random factor		
	F-value	*p-F*	% variance	*z*-value	*p-z*
Plant height	0.45	0.78	6.9	1.12	0.129
Spike length	0.94	0.98	79.0	2.24	0.013
Awn length	0.06	0.98	83.9	2.54	0.012
Spikelets/spike	19.75	0.0001	13.9	1.81	0.035
Seeds/spike	189.80	0.0001	4.4	1.53	0.063
Spike density	1.80	0.19	70.5	2.54	0.005
Seed length	1.09	0.43	14.3	1.93	0.026
Seed width	0.71	0.67	11.9	1.86	0.031
Seed size	0.89	0.51	19.8	2.00	0.022
Kernel weight	0.29	0.87	14.8	1.97	0.024
Days to heading	42.00	0.0001	2.3	1.13	0.160
Days to maturity	7.25	0.005	10.0	1.69	0.045
Filling period	14.38	0.0003	5.6	1.69	0.045
Spike/Plant height	0.78	0.55	78.6	2.55	0.013
Awn/Spike length	0.04	0.96	90.3	2.58	0.004
Spikelet fertility	22.24	0.0001	14.2	1.94	0.012

Table 7. Variance analyses (using landraces as fixed factor) and variance components analyses (using awn color variants as random factor) of phenological and quantitative variables in a wheat landrace from Oman.

Variable	Fixed factor		Random factor		
	F-value	*p-F*	% variance	*z*-value	*p-z*
Plant height	110.20	0.0001	4.8	1.06	0.140
Spike length	0.34	0.84	57.0	2.55	0.005
Awn length	0.29	0.88	59.8	2.54	0.005
Spikelets/spike	24.70	0.0001	10.9	1.98	0.023
Seeds/spike	109.80	0.0001	9.2	1.43	0.075
Spike density	1.80	0.18	50.5	2.54	0.005
Seed length	0.29	0.88	34.4	2.30	0.010
Seed width	2.70	0.07	4.4	1.46	0.070
Seed size	1.32	0.31	14.8	1.96	0.024
Kernel weight	1.20	0.35	26.9	2.26	0.012
Days to heading	8.50	0.001	20.1	2.13	0.016
Days to maturity	4.55	0.014	18.2	1.94	0.025
Filling period	5.12	0.009	22.2	2.16	0.015
Spike/Plant height	0.79	0.55	55.6	2.56	0.005
Awn/Spike length	0.15	0.96	67.3	2.80	0.004
Spikelet fertility	23.40	0.0001	12.2	1.69	0.044

Results of the analyses of variance and variance components analyses when spike awndness was used as a random factor (Table 6) were similar to previous results except for the non-significant plant height. Only six traits expressed significant differences between LR populations; these were, in decreasing order, seeds/spike, days to heading, spikelet fertility, spikelets/spike, filling period and days to maturity. Variance components analysis resulted in the widest range of variances (2.3% for seed width to 90.3% for spike length) being explained by this phenotypic descriptor. However, only five of the 16 quantitative traits have >50% of their variances explained, and only three traits (plant height, seeds/spike and days to heading) were not significant.

Results of the analyses of variance for the fixed factor when using awn color as a random factor (Table 7) were similar to those when spike density was used (Table 5); however, the F-values and level of significance were different. The range in variance being explained by differences between variants of awndness within LRs was large (4.4% for seed width to 67.3% for awn length/spike length ratio). Only five (spike length, awn length, spike density, spike length/plant height ratio, and awn length/spike length ratio) of the 16 traits had >50% of their variances explained by the random factor. Nevertheless, only three traits had non-significant amounts of their variances being explained by the random factor.

Seed color variants (Table 8) were unique among the phenotypic descriptor in accounting for variances in the quantitative traits, although results of the analyses of variance were similar to previous analyses, except that the F-values for some traits were exceptionally large (e.g., seeds/spike and spikelet fertility), while others were extremely small (e.g., seed dimensions and kernel weight). Variance components analysis resulted in a narrow range of variances (1.2% for days to maturity to 52.2% for awn length) being explained by this phenotypic descriptor. However, only one of the 16 quantitative traits have >50% of its variance explained, and none of the z-tests for the quantitative traits were significant.

Results of analyses of variance and variance components analyses using variants of seed vitreousness (i.e., soft, semi-vitreous and vitreous; Table 9) resembled those based on seed color in some aspects and differed from them in other aspects. The same trend in F-values and level of significance was observed as for seed color; however, two additional traits expressed significant differences between LR populations (spike density and spike length/plant height ratio). Also, the same trend was observed for the range of variances being explained by variants of seed vitreousness (1.56% for spikelet fertility to 50.1% for awn length). However, these variants differed from seed color variants by accounting for significant portions of total variance being explained in 11 traits; the z-values for the remaining five traits (plant height, seeds/spike, seed width, kernel weight, and spikelet fertility) were not significant.

Table 8. Variance analyses (using landraces as fixed factor) and variance components analyses (using seed color variants as random factor) of phenological and quantitative variables in a wheat landrace from Oman.

Variable	Fixed factor		Random factor		
	F-value	p-F	% variance	z-value	p-z
Plant height	113.50	0.0004	3.3	1.09	0.14
Spike length	0.56	0.71	43.4	1.54	0.06
Awn length	0.41	0.79	52.2	1.56	0.06
Spikelets/spike	63.30	0.0001	2.3	1.02	0.15
Seeds/spike	314.40	0.0001	1.3	0.55	0.26
Spike dens	2.39	0.18	34.6	1.54	0.06
Seed length	0.31	0.86	17.6	1.46	0.07
Seed width	0.32	0.85	26.5	1.54	0.06
Seed size	0.46	0.77	24.5	1.52	0.06
Kernel weight	0.11	0.97	31.2	1.53	0.06
Days to heading	12.90	0.007	9.7	1.37	0.09
Days to maturity	32.10	0.0009	1.2	0.62	0.26
Filling period	4.80	0.05	10.5	1.39	0.08
Spike/Plant height	1.72	0.28	34.1	1.53	0.06
Awn/Spike length	0.37	0.82	48.2	1.55	0.06
Spikelet fertility	51.10	0.0003	3.6	1.13	0.13

Table 9. Variance analyses (using landraces as fixed factor) and variance components analyses (using seed vitreousness variants as random factor) of phenological and quantitative variables in a wheat landrace from Oman.

Variable	Fixed factor		Random factor		
	F-value	*p-F*	% variance	*z*-value	*p-z*
Plant height	137.60	0.0001	3.1	1.11	0.13
Spike length	0.52	0.72	46.9	2.20	0.02
Awn length	0.47	0.75	50.1	2.20	0.01
Spikelets/spike	33.90	0.0001	8.4	1.68	0.05
Seeds/spike	228.20	0.0001	3.2	1.34	0.09
Spike density	4.56	0.023	40.3	2.14	0.02
Seed length	0.58	0.68	28.5	2.07	0.02
Seed width	2.15	0.14	6.9	1.46	0.07
Seed size	2.05	0.16	13.9	1.85	0.03
Kernel weight	1.33	0.32	10.9	1.39	0.08
Days to heading	16.54	0.0002	10.9	1.62	0.05
Days to maturity	7.52	0.004	15.9	1.85	0.03
Filling period	7.75	0.004	9.2	1.74	0.04
Spike/Plant height	3.60	0.045	33.1	2.10	0.02
Awn/Spike length	0.88	0.51	39.2	2.14	0.02
Spikelet fertility	93.10	0.0001	1.56	0.98	0.16

Phenotypic Diversity Analyses

Two approaches have been pursued to estimate and partition phenotypic diversity in the landrace and its populations; these were estimating the Shannon-Weaver Information Index (*H'*), and estimating total phenotypic diversity and the population differentiation for each LR population as the most important indicator of the value of the germplasm in providing qualitative or quantitative variants that can be used in wheat improvement.

Estimates of the Shannon-Weaver Information Index (*H'*; Table 10) illustrate the wide range of phenotypic variation for each qualitative and quantitative trait (after converting it to categorical trait) averaged for the whole LR and for each LR population. The mean±SD for *H'* averaged over all LR populations were 0.50 and 0.72; and for LR1 (0.36 and 0.66); LR2 (0.37 and 0.69); LR3 (0.43 and 0.67); LR4 (0.47 and 0.69); and LR5 (0.29 and 0.67) populations indicating that there were no significant differences between LR populations. However, when individual traits were considered, large differences in the information index were observed. For example, *H'*-values were the largest for seed/spike in LR2 (0.68) and LR4 populations (0.63) and extremely low for LR5 population (0.02). On the other hand, some traits (e.g., germ size) had consistently small *H'*-values for all LR populations; whereas others (e.g., awn length, kernel weight, and seed size) had consistently large *H'*-values.

The *H'*-values for phenology traits suggested that there were similar levels of phenotypic variation for all three traits at the LR level (*H'*=0.63); however there were a few differences between LR populations. Smaller range was found for *H'*-values for days to heading (0.44-0.59) as compared with days to maturity (0.29-0.61) and filling period (0.31-0.63). Also, the LR populations differed in the magnitude of the *H'*-values for all three phenological traits. For example, LR1, LR3 and LR4 populations had larger *H'*-values for filling period; LR2 had larger *H'*-values for days to maturity than the other two phenological traits; while, LR5 had closer *H'*-values for all three traits.

Estimates of *H'*-values based on quantitative and qualitative assessments of spike density were different, differed in magnitude between LR populations, and, in at least LR3 and LR5 populations, were smaller in magnitude than estimates, and paralleled those for spikelet fertility, with LR5 having the smallest *H'*-values for spikelet fertility and for spike density based on quantitative assessment.

Phenotypic Diversity Analyses (Table 11) indicated that there were a few significant differences between LR populations when averaged over all traits. Total diversity (*H_T*) mean±SD for LR1 (0.489 to 0.539), LR2 (0.509 to 0.559), LR3 (0.526 to 0.556), LR4 (0.567 to 0.597), and LR5 (0.446 to 0.520), which had the largest SD (0.037), suggested that LR4 had the largest *H_T*, but the next largest *G_{ST}* (0.213) after LR5 (*G_{ST}*=0.301); whereas, LR3 had the smallest mean *G_{ST}* estimate (0.144). The range of *H_T* estimates within each LR population was highly different, and the LR

populations displayed different combinations of H_T and G_{ST} estimate for the same trait. The only trait with consistent and low H_T (and its G_{ST} estimates, except for LR5 which was exceptionally the largest) estimates was the germ size, presumably due to the difficulty of categorizing it visually. Small proportions of H_T (~8%) and G_{ST} (~5%) estimates exceeded 0.70; these were for spike density (LR1, LR2 and LR3), seed size (in all except LR1), and spike fertility (LR5); whereas, the majority of G_{ST} estimates for LR1 (57%), LR2

(72%) and LR3 populations (85%) were <0.10 and those for LR4 (14%), and LR5 populations (5%) were exceptionally small. The LR5 population, in spite of its small H_T estimates for germ size, plant height, seed size, and spikelet fertility, seemed to be a rich source of within population variation for these traits as indicated by the large G_{ST} estimates (G_{ST} =0.75, 0.78, 0.72, and 0.93, respectively). Similarly, LR1 population seemed to be a rich source for seed size (G_{ST}=0.84) variation.

Table 10. Shannon's Information Index estimates for a wheat landrace and for each of five populations (LR1 to LR5) within the wheat landrace from Oman.

Variable	All	LR1	LR2	LR3	LR4	LR5
Awndness	0.63	0.56	0.41	0.65	0.65	0.58
Awn color	0.61	0.67	0.42	0.64	0.60	0.53
Glume hairiness	0.51	0.39	0.43	0.48	0.34	0.59
Seed shape	0.52	0.32	0.50	0.56	0.51	0.56
Seed brush	0.61	0.47	0.59	0.56	0.61	0.69
Seed color	0.49	0.48	0.33	0.49	0.50	0.49
Germ size	0.18	0.19	0.22	0.12	0.21	0.16
Vitreousness	0.60	0.54	0.59	0.57	0.59	0.61
Kernel weight	0.64	0.65	0.50	0.64	0.64	0.61
Days to heading	0.63	0.44	0.46	0.55	0.59	0.57
Days to maturity	0.63	0.29	0.65	0.59	0.59	0.61
Filling period	0.63	0.66	0.31	0.63	0.62	0.59
Plant height	0.63	0.35	0.23	0.53	0.52	0.17
Spike length	0.66	0.64	0.62	0.66	0.64	0.57
Awn length	0.70	0.67	0.61	0.69	0.68	0.58
Spikelets/spike	0.65	0.45	0.58	0.52	0.61	0.33
Seeds/spike	0.73	0.33	0.68	0.40	0.63	0.02
Spike density (quantitative)	0.57	0.71	0.69	0.42	0.53	0.29
Spike density (qualitative)	0.71	0.67	0.74	0.53	0.70	0.59
Seed size	0.73	0.65	0.73	0.73	0.71	0.72
Spikelet fertility	0.71	0.57	0.64	0.52	0.69	0.32
Mean	0.61	0.51	0.53	0.55	0.58	0.48
SD	0.11	0.15	0.16	0.12	0.11	0.19

Table 11. Diversity components (Total diversity, Ht and population differentiation, Gst) analyses for each of five populations (LR1 to LR5) in a wheat landrace from Oman.

Variable	LR1		LR2		LR3		LR4		LR5	
	H_T	G_{ST}	H_T	G_{ST}	H_T	G_{ST}	H_T	G_{ST}	H_T	G_{ST}
Awndness	0.56	0.05	0.42	0.07	0.65	0.03	0.64	0.18	0.58	0.20
Awn color	0.67	0.05	0.43	0.04	0.64	0.03	0.60	0.06	0.53	0.13
Glume hairiness	0.40	0.08	0.53	0.04	0.47	0.05	0.32	0.29	0.59	0.22
Seed shape	0.31	0.07	0.51	0.04	0.56	0.03	0.52	0.13	0.57	0.44
Seed brush	0.47	0.09	0.59	0.03	0.56	0.02	0.61	0.20	0.69	0.23
Seed color	0.48	0.12	0.33	0.08	0.49	0.04	0.49	0.23	0.50	0.31
Germ size	0.19	0.18	0.22	0.04	0.12	0.09	0.21	0.06	0.15	0.75
Vitreousness	0.53	0.07	0.59	0.06	0.57	0.08	0.58	0.07	0.60	0.31
Kernel weight	0.65	0.09	0.50	0.08	0.64	0.07	0.64	0.10	0.61	0.22
Days to heading	0.43	0.08	0.46	0.05	0.55	0.03	0.59	0.10	0.58	0.34
Days to maturity	0.28	0.19	0.65	0.06	0.59	0.08	0.58	0.18	0.61	0.12
Filling period	0.66	0.05	0.31	0.09	0.63	0.03	0.62	0.17	0.59	0.28
Plant height	0.34	0.62	0.22	0.18	0.52	0.22	0.51	0.26	0.18	0.78

Table 11. Contd..

Variable	LR1	LR2	LR3	LR4	LR5	Variable	LR1	LR2	LR3	LR4
Spike length	0.64	0.09	0.63	0.06	0.66	0.06	0.62	0.23	0.56	0.19
Awn length	0.67	0.06	0.61	0.08	0.68	0.02	0.68	0.13	0.58	0.21
Spikelets/spike	0.45	0.54	0.57	0.14	0.52	0.03	0.61	0.21	0.34	0.36
Seeds/spike	0.34	0.49	0.68	0.21	0.40	0.07	0.62	0.10	0.15	0.31
Spike density (qnt)	0.71	0.02	0.69	0.07	0.42	0.05	0.53	0.18	0.28	0.06
Spike density (qlt)	0.67	0.22	0.74	0.27	0.52	0.08	0.70	0.11	0.59	0.27
Seed size	0.64	0.84	0.73	0.37	0.74	0.24	0.71	0.11	0.72	0.72
Spikelet fertility	0.58	0.32	0.65	0.11	0.51	0.19	0.70	0.19	0.31	0.93
Mean	0.512	0.191	0.534	0.187	0.541	0.144	0.582	0.213	0.483	0.301
SD	0.023		0.025		0.015		0.015		0.037	

Hierarchical and joint clustering

Clustering of LR populations and sub-samples within populations, on the Y-axis, and phenotypic, quantitative and qualitative traits, on the X-axis (Figure 7) offered valuable insights into the level of relatedness/distances between sub-samples within LR populations, distances between LR populations and relatedness between groups of traits; and how traits within sub-samples and within LR populations are structured. Each five sub-samples within LR population clustered at the smallest distance, LR3 and LR4 populations were the first two populations to cluster at about 20 Euclidean distances, then these populations clustered with LR5 to form one large cluster at about 50 Euclidean distances. On the other hand, LR1 and LR2 formed a cluster at about 60 Euclidean distances and joined the other cluster at the maximum distance of 100. Almost in each LR population there was one sub-sample that clearly clustered at a larger distance within the LR population than the remaining sub-samples; however, in LR5, two of these sub-samples joined the remaining three at a larger distance.

The hierarchical clustering of traits on the Y-axis (Figure 7) resulted in the formation of four major clusters, the first three of which joined the fourth at the largest distance. Different combinations of traits formed these clustered and were associated with sub-samples within LR populations. For example, starting from the left-hand side of Figure 7, the first cluster was formed by the hierarchical joining of grain yield per plant with spike density, then these two traits joined awndness and seed color, and finally vitreousness completed the hierarchical cluster. The last cluster (at the far right-hand side of Fig. 8) is more complex and was formed by the hierarchical joining of several phenological, quantitative and qualitative traits and was the last to join the remaining clusters in this analysis.

Relatedness between traits and sub-samples within each LR population was expressed as a color-coded scheme and was expressed in standardized units for valid comparisons between and within trait variants. The classification scale ranged from 0.7 to -2.3. Sources of high, medium, and large levels of single or multiple traits and their association with certain LR populations can be identified for comparative purposes and to identify which sub-samples or LR populations are potential sources of single or multiple traits. For example, LR2 and LR4 offer large values for seeds/spike and spikelets per spike, as well as spike density (whether expressed as qualitative or quantitative traits). Sources of tightly-linked groups of traits can also be identified based on the standardized scale. For example, large values of days to heading and to maturity were associated with glumes with dense hairs in LR1; whereas, LR3 offered the opposite levels of variants of the same traits and LR2 offered the intermediate variants.
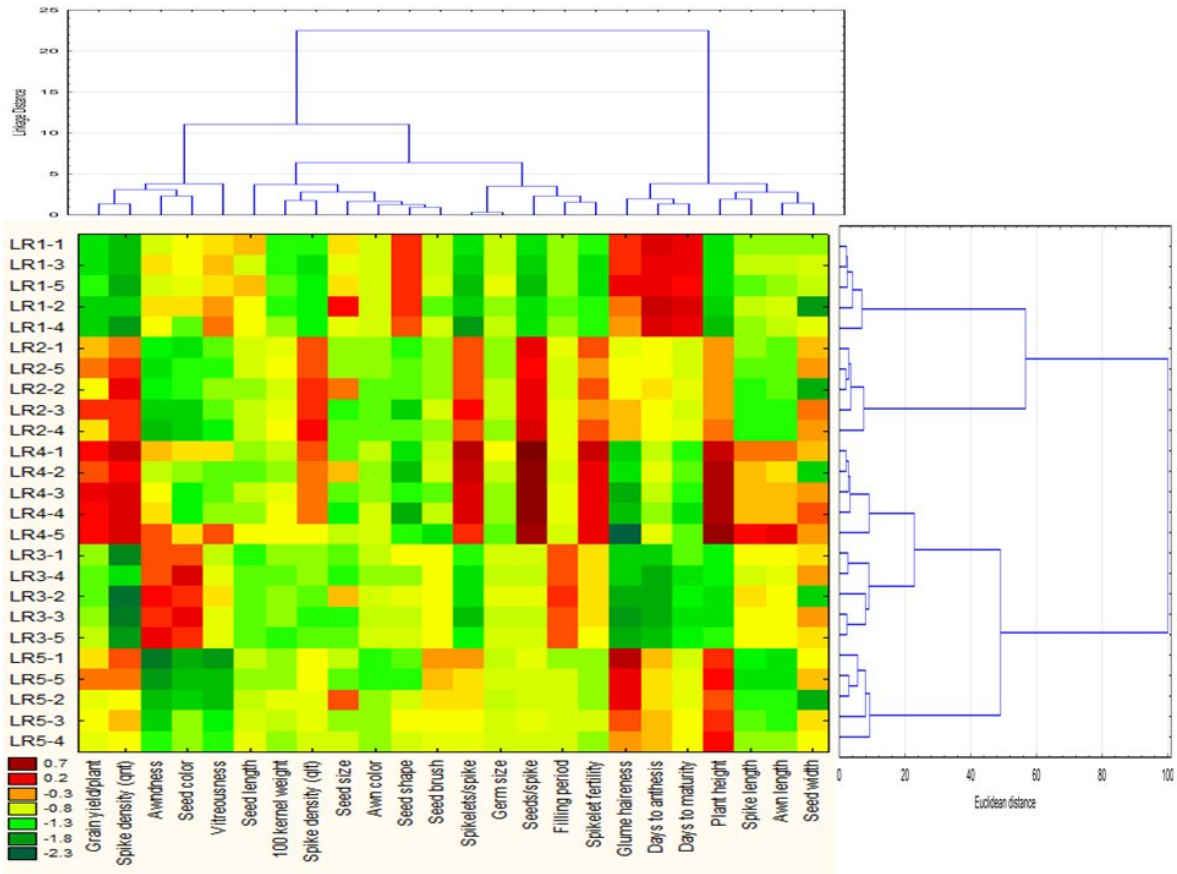
Figure 7. Hierarchical and joint cluster analyses of five sub-samples (-1 to -5) derived from each of five landrace populations (LR1 to LR5; Y-axis) and 24 standardized phenological, quantitative and qualitative traits measured or recorded on 800 plants of a wheat landrace from Oman.

Yield prediction

Two methods were used to assess grain yield per plant for the whole LR and for each LR population. In the first method, we used the first and second canonical discriminant function, which accounted for 72 and 18% of total variation, respectively, to estimate spikelet fertility, as an important yield component of grain yield per plant (Figure 8). In the second method, we used (1) phenological and quantitative traits (Table 12) and (2) qualitative traits (Table 13), separately, to construct structural equation models and estimate direct and indirect effects of these traits on grain yield per plant.

The linear equation predicting spikelet fertility as a function of the first canonical discriminant root

(CDR1; Figure 8A) indicated that the relationship between these two variables was negative and highly significant ($r = -0.66$; $p<0.0001$). However, only 43% of the variation in spikelet fertility can be explained by the variation in plant traits contributing to CDR1 (Table 3). The second root (CDR2) was positively and significantly correlated with spikelet fertility ($r = 0.49$; $p<0.0001$); however, it only explained 24% of its variation. Some of the traits that contributed to CDR1 also contributed to CDR2 (Table 3); however, and as indicated earlier, CDR2 explained a small portion (12%) of total variation in the whole set of phenological, quantitative and qualitative traits during canonical discriminant analyses.
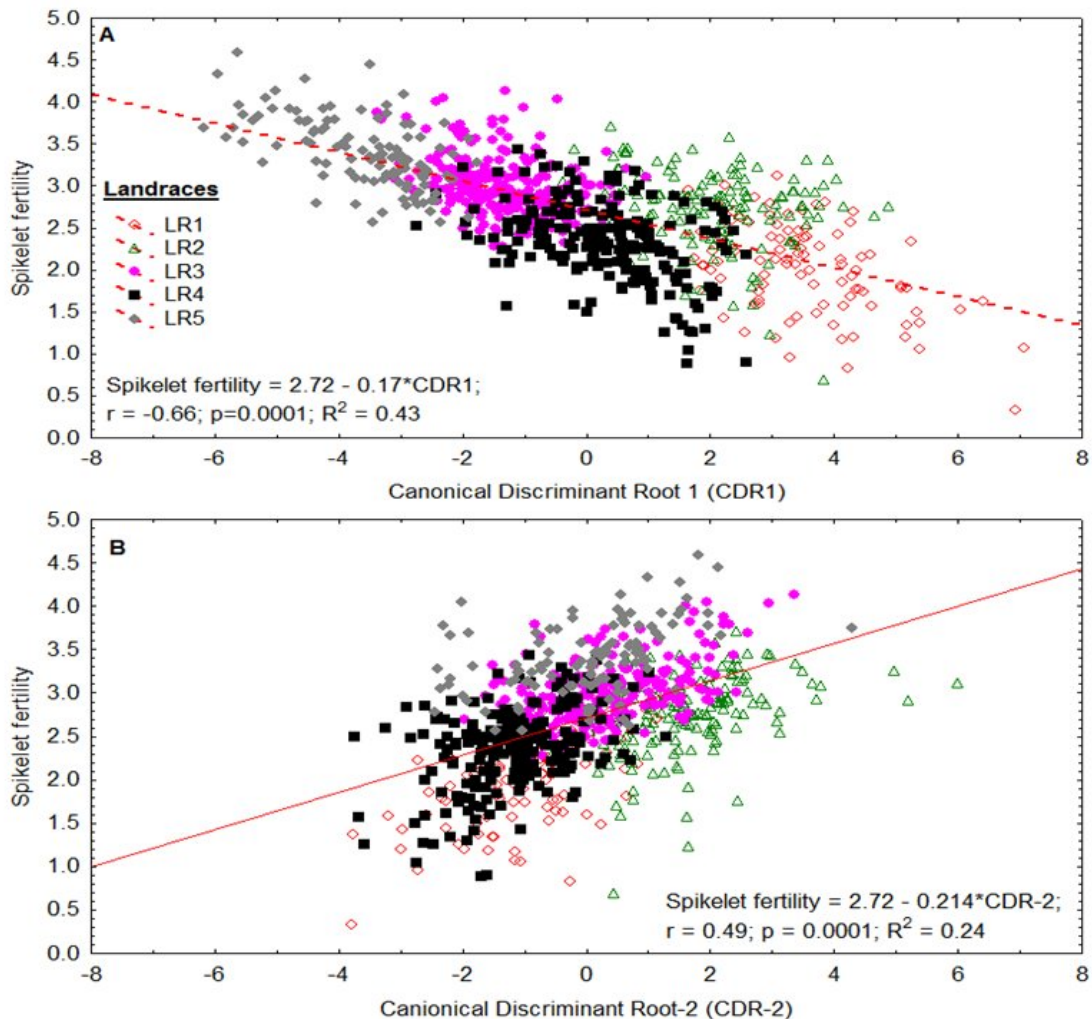
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Figure 8. Linear relationships between spikelet fertility and each of the first canonical discriminant root, CDR-1, (A) and second CDR-2 (B) in five populations (LR1 to LR5) of a wheat landrace from Oman (See standardized coefficients in Table 3 for details).

Structural Equation Modeling (SEM)

The SEM models based on quantitative (Table 12) and qualitative (Table 13) traits for the whole LR germplasm collection was highly significant (p<0.01), based on a Maximum Likelihood χ^2 test, and will not be discussed further; however, separate SEM models using quantitative data (Table 12) for each LR population were not significant ($p = 0.62$ for LR5 to 0.83 for LR1) and, therefore, each one fits the data for a particular LR population. For each LR population, we constructed four latent variables (i.e., architecture, phenology, fertility and yield), estimated the dependence (regression coefficient) between individual traits (manifest variables) and their respective latent variable, estimated the variance for each manifest variable, then estimated covariances between pairs of latent variables, with yield as the latent variable of interest.

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Table 12. Results of the structural equation modeling for grain yield per plant as a function of phenological and quantitative traits in a wheat landrace from Oman (non-significant parameter estimates are *in italics*).

Effect	Path		All	LR1	LR2	LR3	LR4	LR5
Relationship	Latent	Manifest	Parameter estimate ($p<0.05$)					
Dependence	Architecture	Plant height	*0.07*	0.54	0.68	0.68	0.15	0.29
		Spike length	*0.05*	0.43	0.50	0.51	0.94	0.51
		Awn length	0.84	0.47	0.62	0.62	0.51	0.95
	Phenology	Days to heading	*0.11*	0.60	0.61	0.60	0.62	0.61
		Days to maturity	0.43	0.53	0.69	0.69	0.56	0.57
		Filling period	-0.69	-0.48	-0.91	-0.53	-0.81	-0.82
	Fertility	Spikelets/spike	0.84	0.52	0.54	0.58	0.41	0.95
		Spike density	0.69	0.51	0.66	0.67	0.58	0.45
		Seeds/spike	0.78	0.53	0.63	0.63	0.52	0.49
	Yield	Seed size	-0.24	0.64	0.74	0.74	0.74	*0.04*
		Kernel weight	0.19	-0.79	-0.80	0.64	0.17	*-0.09*
		Grain yield/plant	0.95	0.71	0.54	0.53	0.97	0.54
Variance		Plant height	0.99	0.71	0.54	0.54	0.97	0.75
		Spike length	*0.00*	0.82	0.75	0.75	0.12	0.53
		Awn length	0.31	0.77	0.61	0.61	0.61	0.74
		Days to heading	0.00	0.64	0.64	0.64	0.63	0.61
		Days to maturity	0.82	0.72	0.52	0.52	0.52	0.52
		Filling period	0.53	0.76	0.72	0.72	0.35	0.74
		Spikelets/spike	0.31	0.73	0.66	0.66	0.83	0.67
		Spike density	0.52	0.74	0.55	0.56	0.56	0.56
		Seeds/spike	0.39	0.73	0.61	0.61	0.73	0.61
		Seed size	0.94	0.59	0.45	0.45	0.45	0.45
		Kernel weight	0.96	0.44	0.59	0.59	0.59	0.59
		Grain yield/plant	*0.01*	0.85	0.71	0.71	0.71	0.71
Covariance	Architecture	Phenology	*0.06*	0.15	-0.25	0.17	0.19	*-0.05*
		Fertility	*0.12*	0.17	0.25	0.15	0.12	0.14
		Yield	*-0.05*	0.43	0.15	0.38	0.35	0.21
	Phenology	Fertility	0.75	0.85	0.67	0.45	0.57	0.54
		Yield	0.65	0.45	0.76	0.54	0.56	0.73
	Fertility	Yield	0.52	0.63	0.77	0.59	0.61	0.83
Maximum Likelihood χ^2			221.5	43.9	49.8	50.1	44.58	49.4
Degrees of freedom			54	54	54	54	54	54
p-value			0.01	0.83	0.64	0.64	0.80	0.62
RMS standard residual			0.211	0.07	0.08	0.07	0.07	0.09

All parameter estimated (i.e., dependence, variance and covariance coefficients) were significant ($p<0.05$) except the manifest variables seed size and kernel weight, and the architecture-phenology covariance in LR5. Additionally, all estimated parameters were positive except the dependence relationship between filling period and the latent variable phenology in all LR populations, the dependence relationship between kernel weight and yield in LR1 and LR2 populations, and the covariance between the latent variables architecture and phenology in LR2 population. We present detailed results on covariances of latent variables and how they affect yield as represented by the manifest variables: seed size, kernel weight, and grain yield per plant. Covariances between architecture and phenology, although statistically significant and positive (except for LR2 and LR5 populations), they were small in magnitude; the same can be stated for architecture and fertility, except that all estimates were positive. There were sizable differences across LR populations for phenology-fertility (0.45 for LR3 and LR5 to 0.85 for LR1 population), phenology- yield (0.45 for LR1 to 0.73 for LR5 population), and fertility-yield (0.59 for LR3 to 0.83 for LR5) covariances. Separate SEM models using qualitative data (Table 13) for each LR population, and based on a Maximum Likelihood χ^2 test, were not significant ($p = 0.06$ for each of LR4 and LR5 to 0.58 for LR1), therefore, each SEM model fits the data for the particular LR population. For each LR population, we constructed four latent variables (i.e., phenotype, color, shape and yield), estimated

the dependence (regression coefficient) between individual traits (manifest variables) and their respective latent variable, estimated the variance for each manifest variable, then estimated covariances between pairs of latent variables, with yield as the latent variable of interest.

A comparable number of negative coefficients were found using qualitative data as predictors of grain yield; these were mostly within the dependence part of the SEM model (i.e., germ size, vitreousness and seed shape in LR1, and spike density in LR2 and LR4 populations) and only three in the covariance part of the models (phenotype-shape and color-shape in LR1, and phenotype-color in LR2 population). As in the case of quantitative SEM models, we present detailed results on covariances of latent variables and how they affect yield as represented by grain yield per plant as the only manifest variable. The phenotype-shape in LR2, the shape-yield covariance estimates across LR populations, as well as the color-yield covariance estimates for LR2 and LR3, were not significant. The LR2 population differed from the rest in having a negative parameter estimate for the phenotype-color; similarly, negative phenotype-shape, and negative color-shape parameter estimates for LR1 were negative. The phenotype-yield covariance estimates were large and positive for all LR populations, as well as the color-yield covariance for LR1, LR4 and LR5 populations.

Table 13. Results of the structural equation modeling for grain yield per plant as a function of qualitative traits in a wheat landrace from Oman (non-significant parameter estimates are *in italics*).

Effect	Path		All	LR1	LR2	LR3	LR4	LR5
Relationship	Latent	Manifest	Parameter estimate (p<0.05)					
Dependence	Phenotype	Spike density	-0.25	*0.07*	-1.00	0.31	-0.28	0.14
		Awndness	1.00	1.00	0.46	-0.39	0.51	0.51
		Germ size	*-0.08*	-0.32	0.52	0.56	0.37	-0.29
	Color	Awn color	0.69	0.89	*-0.12*	0.24	0.74	0.48
		Seed color	0.46	0.63	0.71	0.50	0.59	0.73
		Vitreousness	0.15	-0.54	0.78	0.76	*0.07*	0.87
	Shape	Glume hairiness	0.63	0.63	*0.05*	0.46	*-0.03*	0.80
		Seed shape	-0.15	-0.48	0.61	-0.20	0.68	*-0.11*
		Seed brush	0.16	0.25	0.24	0.68	0.18	0.65
	Yield	Grain yield/plant	0.63	*0.35*	0.71	*-0.16*	*-0.09*	0.51
Variance		Spike density	0.94	0.99	0.00	0.90	0.69	0.69
		Awndness	0.00	0.00	0.78	0.85	0.74	0.74
		Germ size	0.99	0.89	0.73	0.68	0.86	0.86
		Awn color	0.52	0.21	0.98	0.95	0.45	0.45
		Seed color	0.79	0.60	0.50	0.75	0.54	0.54
		Vitreousness	0.97	0.71	0.39	0.42	0.67	0.68
		Glume hairiness	0.61	0.61	0.99	0.79	0.78	0.67
		Seed shape	0.98	0.77	0.63	0.96	0.53	0.53
		Seed brush	0.97	0.94	0.94	0.54	0.62	0.62
		Grain yield/plant	0.61	0.88	0.82	0.97	*0.43*	*0.44*
Covariance	Phenotype	Color	*1.00*	0.84	-0.65	0.81	0.34	0.34
		Shape	*-1.00*	-0.88	*0.08*	0.74	0.59	0.60
	Color	Shape	*-0.69*	-0.56	0.43	0.73	0.47	0.47
	Phenotype	Yield	*-0.11*	0.77	0.52	0.51	0.62	0.62
	Shape	Yield	*-0.01*	*0.58*	*0.12*	*0.51*	*0.51*	*0.51*
	Color	Yield	0.08	0.74	*0.56*	*-0.42*	0.63	0.62
Maximum Likelihood χ^2			807.3	27.8	22.8	38.9	45.2	45.2
Degrees of freedom			30	30	30	30	30	30
p-value			0.01	0.58	0.34	0.61	0.06	0.06
RMS standard residual			0.116	0.07	0.06	0.05	0.05	0.06

Discussion

Since the early 1970s, massive collecting efforts have been carried out in response to the fear of the disappearance of traditional cultivars and landraces of major crops, including wheat, in the wake of developments triggered by the Green Revolution (DeLacy et al., 2000). The question, yet to be answered, however, is how much crop diversity was lost at the time of shift from landraces and old varieties to modern varieties (Tsegaye and Berg, 2007; Van de Wouw et al., 2009; 2010)? Already Baur in1914 (*c.f.* Van de Wouw et al., 2010) warned of the consequences of the disappearance of traditional landraces for the future of plant breeding. Since genetic erosion of landraces, including those of wheat, has been inadequately tracked, the resulting uncertainty about their future has a potentially large impact on our ability to value and use them in a sustainable manner (Brush and Meng, 1998). The genetic erosion caused by the displacement of wheat landraces in developing countries (Van de Wouw et al., 2009), including Oman (Guarino, 1990; Gebauer et al., 2010), is a concern for wheat breeders because these genetic resources may be the most valuable sources for broadening the genetic bases for many traits in current and future wheat breeding and improvement programs. While the problem was globally addressed, to some extent, by international strategy of collecting, conserving and utilization of wheat landraces (Bradsley and Thomas, 2005; Goats and Bockelman, 2012), specific efforts to identify potentially new genetic variability for immediate use in breeding programs are still needed at local levels, especially in the developing world (Akram et al., 2012; Ahmad et al., 2013; Jaradat, 2013). Local landraces may provide new alleles for the improvement of commercially valuable traits in wheat, including quality traits and adaptation to biotic and abiotic stresses (Yedliay et al., 2011; Goats and Bockelman, 2102). Introgression of genes or gene blocks conferring these traits into modern cultivars can be very useful, especially when breeding and developing new wheat cultivars for use by subsistence farmers in sub-optimal environments (Masood et al., 2005; Tsegaye and Berg, 2007).

Collection missions carried out by the Omani Ministry of Agriculture resulted in collecting and characterization of a number of wheat landraces including Sarraya, Walidi, Cooley, Greda, Missani and Hamira (Al-Maskri et al, 2003). As was the case in the current LR populations (Table 1; Fig. 1), and other parts of the Old World, such as the Indian subcontinent (Akram et al., 2012) and Ethiopia

(Bechere et al., 1996; Tsegaye and Berg, 2007), the morphological characterization of these landraces revealed that they were often composed of mixtures of bread wheat and durum wheat and comprising several botanical varieties. Such landraces may have been retained simply because they meet local socioeconomic, cultural and ecological niches (Bardsley and Thomas, 2005). However, the indirect evidence derived from earlier studies, indicated that cultivation of these landraces is declining and the need is urgent for more appropriate strategies for their conservation (Jaradat, 2006; Van de Wouw et al., 2009). Appropriate forms of on-farm conservation need to be developed in relation to both local cultural values attributed to these genetic resources, and within the context of Oman's agricultural development objectives. However; the main difficulties of on-farm conservation of landraces are non-biological, but rather a complex of ethano-anthropological processes, involving legal, economic and social factors, superimposed on ecological and genetic processes (Jaradat, 2013). The Omani wheat landraces have been described (Zhang et al., 2006) as being quiet unique and different from those collected in other regions, while harboring a comparable level of genetic diversity. Therefore, more wheat landraces from the country should be collected. The geographic isolation and the limited exchanges of wheat seed among oases suggest that wheat landraces may widely differ among various oases. In the current study, we found landrace populations characterized by large diversity at different hierarchal levels. These populations were subjected to natural, and probably man-made, selection; were not subjected to modern improvement methods; and were managed by subsistence, resource-poor farmers in a marginal zone for wheat production (Al-Maskri et al., 2003; Al-Khanjary et al., 2007; 2008; Gebaur et al., 2010). We concluded that these landrace populations, similar to other landraces in the primary (Ali Deb et al., 1992; Karagöz and Zençirçi 2005; Ahmadizadeh et al., 2011; Jaradat, 2013) and secondary (Bechere et al., 1995; 1996) centers of wheat diversity, can provide a largely unexplored diversity with great potential for broadening the genetic base of modern wheat cultivars.

Classical univariate analysis procedures, limited to estimation and hypothesis testing, are not capable of detecting patterns and exploring multivariate data structures in germplasm characterization and evaluation, genetic resources studies, or in evaluating large numbers of breeding

lines and cultivars. Therefore multivariate analysis procedures to classify, characterize, evaluate and order large numbers of germplasm material, trait combinations and genetic variation are gaining considerable importance and assuming considerable significance. Earlier studies (Al-Khanjari et al., 2007; 2008) confirmed the existence of surprisingly high levels of genetic diversity in Omani wheat landraces as already concluded from previous morphological analysis and showed that molecular markers can be used for landrace analyses and provide a means for a more detailed diversity evaluation. The high genetic diversity in the Omani durum and bread wheat landraces (Hammer et al., 2004; Gebauer et al., 2010) is most likely the result of their long history of cultivation in relatively isolated mountain oasis systems which enhanced the effects of natural and artificial selection on germplasm diversity. High diversity in traditional landraces from Oman likely reflects the effects of the germplasm old selection history and of the many agro-environments in remote mountain oases (Gebauer et al., 2010).

Taller straw and awnless or awnletted spikes (Fig. 2-6) are important characteristics in some of the LR populations for their use as livestock feed. However, landraces may have some undesirable traits, such as susceptibility to lodging and low average yields. Nevertheless, they are retained because they are a low risk option under marginal conditions, resulting in fewer poor production years. Phenotypic diversity, assessed by Shannon-Weaver Information Index or by population differentiation in the landrace populations, indicated some similarities and major differences in the level of polymorphism within and among this germplasm. Similar studies on landraces from Ethiopia (Belay et al., 1993; Bechere et al, 1996), Iran (Moghaddam et al., 1997), Jordan (Jaradat, 2006), and Spain (Moragues et al., 2006), for example, reported large levels of polymorphisms for phenological, quantitative and quanlitative traits. Most traits of durum wheat landraces from Ethiopia were polymorphic; however, monomorphism was common in many of the populations for dense spikes, glume long beak, and glabrous glumes (Bechere et al., 1996). Another group of Ethiopian wheat landraces were late for days to heading and days to maturity, and had shorter grain filling period, lower fertility and lower 100-seed weight than high-yielding varieties (Belay et al., 1993).

Different levels of within-phenological trait associations (i.e., days to heading, days to maturity

and filling period) and their associations with other plant- spike- or seed-traits in these landrace populations exceeded those reported earlier. For example, in Ethiopian wheat landraces (Belay et al., 1993), There were very strong associations between days to heading and days to maturity; these two traits showed negative association with the rest of traits under study; whereas, grain filling period showed a significant positive association with number of kernels per spike and with 100-kernel weight but not with grain yield per plant as was the case in the current study. Moreover, genetic variation for traits conducive to crop competitiveness against weeds may be concentrated in landraces that were selected before the widespread use of crop protection chemicals (Murphy et al., 2008). It was postulated that the differences in the life history strategy between the old and modern cultivars were attributed to the reduced competitive ability in the modern cultivars which led to increased yield of the crop population and greater yield stability (Fang et al., 2011). This yield stability can be achieved in wheat landraces by developing "new" landraces with less competition between genotypes.

We used the more advanced structural equation modeling (SEM; Lamb et al., 2011), rather than using the classical path analysis (Ahmadizadeh et al., 2011) because SEM is theory oriented as opposed to hypothesis oriented; has the capacity to represent hypotheses about causal networks; can be used to test between competing models; and has a value as a framework for interpretation when there are large number of predictors and responses with complex causal connections as demonstrated by the two models we developed for wheat yield (Table 12 and 13). The latent variables constructed from manifest variables provided much more advanced options, including the specification of measurement error and the separation of the mechanics of measurement and observation from the conceptual questions under study. Such models may be used as research tools to identify additional paths to each model that may reveal novel biological hypothesis that can be explored and refined through follow-up research. Clear differences (or similarities) between LR populations in parameter estimates and their positive or negative association with latent variables may indicate the presence of alternative strategies in yield components compensation, and the different possibilities of arriving at the same grain yield using alternative trait associations. Such changes in yield components, for example, occurred even during the movement of durum wheat from East to West through the north side of

the Mediterranean basin (Moragues et al., 2006). These researchers concluded that grain weight and number of spikes per unit area may be selection criteria to improve adaptation for the northern and southern parts of the Mediterranean basin, respectively. Although not explored in this study, it is speculated that there is a potential for aroma and flavor diversity in wheat landraces; therefore, there is potential for production of aromatic, high-quality bread wheat in both modern and wheat varieties and older land races (Starr et al., 2013).

The phenotypic and statistical evidence reported on a barley landrace from Oman (Jaradat et al., 2004) suggested that farmers' selection for desirable agronomic traits is a major force shaping the dynamics of crop plant populations in subsistence agriculture in that country; and that the on-farm conservation of these landraces ensures the continuation of this dynamic process. Such landraces could be improved by inter-crossing the promising genotypes, with simultaneous selection for earliness, fewer numbers of spikes per plant, greater number of grains per spike, and heavier grains (Moghaddam et al., 1997).

Conclusions

Traditional wheat farmers contributed, for thousands of years, to the wealth of variation available in landraces that was used to improve wheat yield and adaptation in different parts of the world. We identified large level of variation in a wheat landrace managed by subsistence farmers and grown under marginal wheat production environment. We suggest that farmers grow and maintain highly variable wheat landraces to lower the risk of failure under marginal production conditions and to increase food security of isolated communities. However, additional information on the factors contributing to the private value which farmers assign to wheat landraces is needed and may help to identify a strategy for ensuring the conservation of their genetic resources; such information is needed to assess the likelihood that particular farmers will continue to maintain landraces. The statistical analyses procedures used in this study are of value to students and professionals working in the field of genetic resource conservation and utilization. The landrace populations identified in the study are valuable sources of traits for adaptation to marginal wheat-growing parts of the world with high temperature and salinity, and may have gene complexes to combat climate change. In an attempt to answer the question posed by this study, it is pertinent to conclude that farmer-managed wheat landraces are highly diverse based on the in-depth analyses of the data, and as supported by results of earlier studies. Utilization of this genetic diversity, however, requires systematic evaluation of many traits, especially those of quality significance and those that confer adaptation to climate change.

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