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EDITORIAL

The Value of Wheat Landraces

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Whether man was domesticated by wheat, or wheat was domesticated by man is but two faces of the same coin; both incidents marked a turning point in human history and led to the emergence of human civilization in the Fertile Crescent of the Old World. The complex history of wheat domestication from its progenitor, wild emmer wheat, followed by the evolution of domesticated durum, then bread wheat, and the subsequent development of a multitude of wheat landraces, testify to the ingenuity of those early “farmers” who recognized its potential, as a food crop, among the swarms of grasses that once covered that part of the world.

Ever since its domestication, and throughout the last ~10,000 years, farmers have been behind the development, improvement and on-farm conservation of wheat genetic diversity, mostly as landraces. Thousands of years of cultivation aided by natural and human selection have resulted in the evolution of immense diversity in wheat. A number of socio-cultural factors, food traditions, and agro-ecological environments in the Old World favored the cultivation and utilization of diverse wheat genetic resources constituting what is now known as landraces. Each wheat landrace has particular significance in the food culture, as a source of daily diet, and of food and drink for special occasions.

Wheat landraces can be considered as an evolutionary link between wild emmer wheat and modern-day wheat cultivars. Recently, however, many wheat landraces have been lost due to the introduction of modern wheat varieties, disappearance of traditional farming systems, the aging and exodus of rural population, and accelerated environmental degradation. Wheat landraces have been largely replaced, in their centers of diversity by monocultures of modern varieties, which are pure genotypes. This genetic erosion resulted in significant loss of valuable genetic diversity for quality traits and resistance or tolerance to biotic and abiotic stresses; whereas, the pure wheat genotypes do not have the wide adaptation and the diverse genetic background already present in landraces. Climate change is expected to differentially affect components of complex biological interactions in modern and

traditional wheat production systems. Wheat yield and quality will be affected directly and indirectly by climate change. The manner with which wheat landraces and their populations in and outside their centers of diversity might respond to climate change will determine their continued productivity, utility, and survival for the benefit of humanity.

Traditional management of wheat landraces contributed more to the conservation of a general level of diversity, as a source of sustenance and sustainability, than to the conservation of genetically stable and distinct populations. Wheat landraces embody not only diverse alleles and genotypes, but also evolutionary processes such as gene flow between different populations, mainly via seed exchange and local knowledge systems such as folk taxonomies and information about selection for specific quality attributes or for heterogeneous environments.

Characterization of the population structure of wheat landraces is critical to identifying and correctly interpreting the association between their functional and molecular diversities. Such information is essential to utilize landraces as donors of traits in wheat breeding, to define the areas of adaptation of different landraces, to identify priority areas for on-farm conservation, and to understand the genetic consequences of the interaction between climate change, growing environments and farmers' practices.

The objective of this special issue of The Emirates Journal of Food and Agriculture was to provide a forum for wheat scientists to exchange research results and forge joint research plans, exchange germplasm and revive global interest in wheat landraces. The manuscripts published in this special issue are a contribution towards this effort. It is hoped that EJFA will continue its endeavor by encouraging scientists to collect, conserve, research and utilize the wealth of genetic diversity in the remaining wheat landraces, whether stored in genebanks or tended by resource-poor farmers throughout the world.

It was a pleasure working with the authors and with the editorial staff to bring this information to the reader of The EJFA.

REGULAR ARTICLE

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 subdivided 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).

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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., 2003; Al-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 Zencirçi, 2005; Zencirçi 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 Zencirçi, 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 heterogeneous 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, awnness, 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); Awnness: 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 Levene 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 awnness, 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) $\leq \text{mean} - 1.0 \text{ SD}$., (medium) $> \text{mean} - 1.0 \text{ SD} < \text{mean} + 1.0 \text{ SD}$., and (Large) $\geq \text{mean} + 1.0 \text{ SD}$] 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:

$$H' = - \sum p_i \ln p_i \text{ for } i = 1, 2, \dots, n.$$

Where p_i is the relative frequency i th category of the j th 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 misclassification, and the overlap between LR populations, was found between LR3 and LR4; whereas, 21% of entries in LR5 were misclassified 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 ($p < 0.05$).

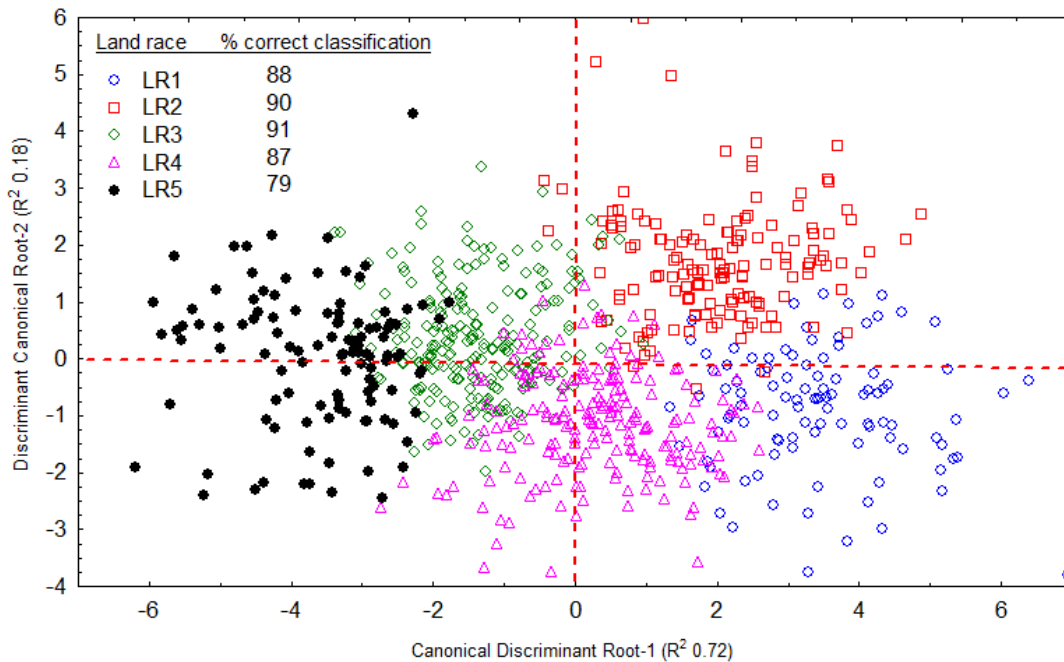


Figure 1. Canonical Discriminant analyses between five populations (LR1 to LR5) and percent correct classification of these landrace populations based on phenological, quantitative and qualitative traits in a wheat landrace from Oman. (See Table 2 for details)

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 (awnness) 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 coefficient 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
Awnness	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 discriminant 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 awnness (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 awnness (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.

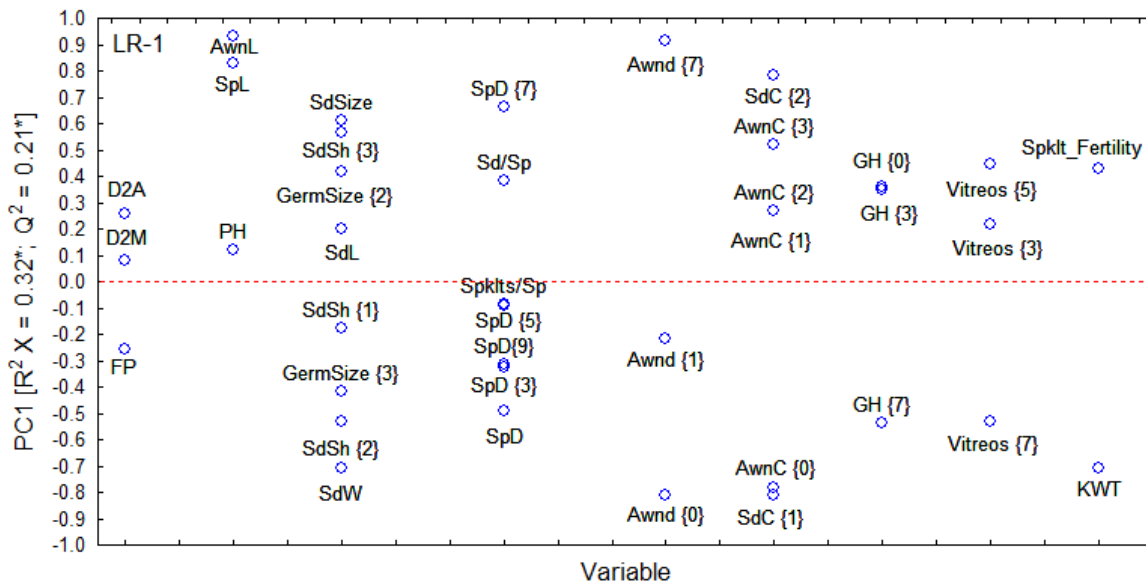


Figure 2. The first principal component (PC1) and coefficients of determination at the prediction (R^2) and validation (Q^2) phases of PC model building derived from phenological, quantitative and qualitative traits in the first population (LR1) in a wheat landrace from Oman.

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.

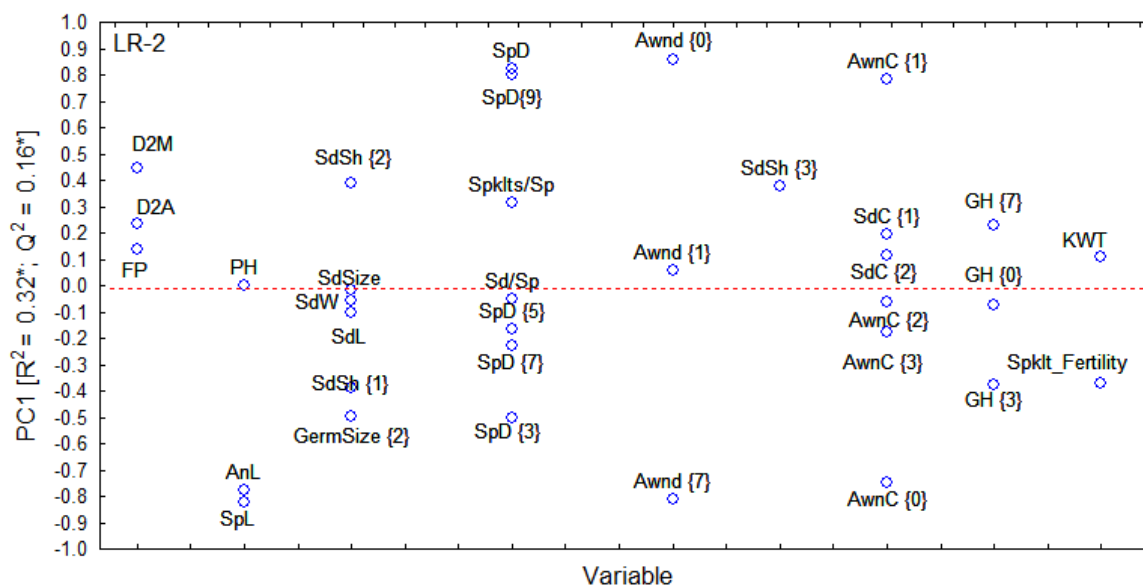


Figure 3. The first principal component (PC1) and coefficients of determination at the prediction (R2) and validation (Q2) phases of the PC model building derived from phenological, quantitative and qualitative traits in the first population (LR2) in a wheat landrace from Oman.

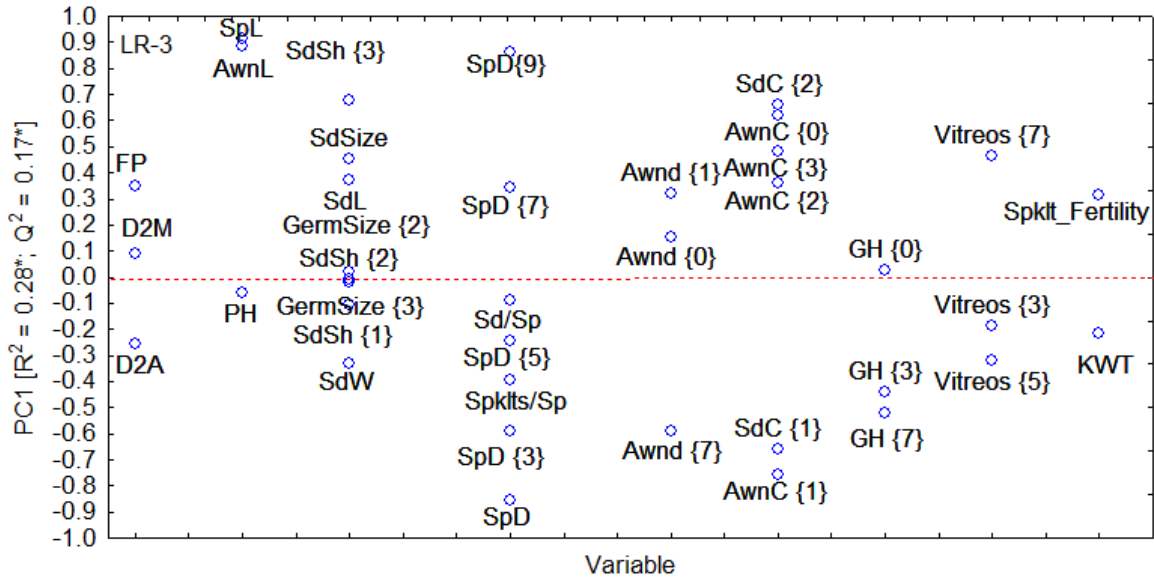


Figure 4. The first principal component (PC1) and coefficients of determination at the prediction (R2) and validation (Q2) phases of the PC model building derived from phenological, quantitative and qualitative traits in the first population (LR3) in a wheat landrace from Oman.

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

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, respectively (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.

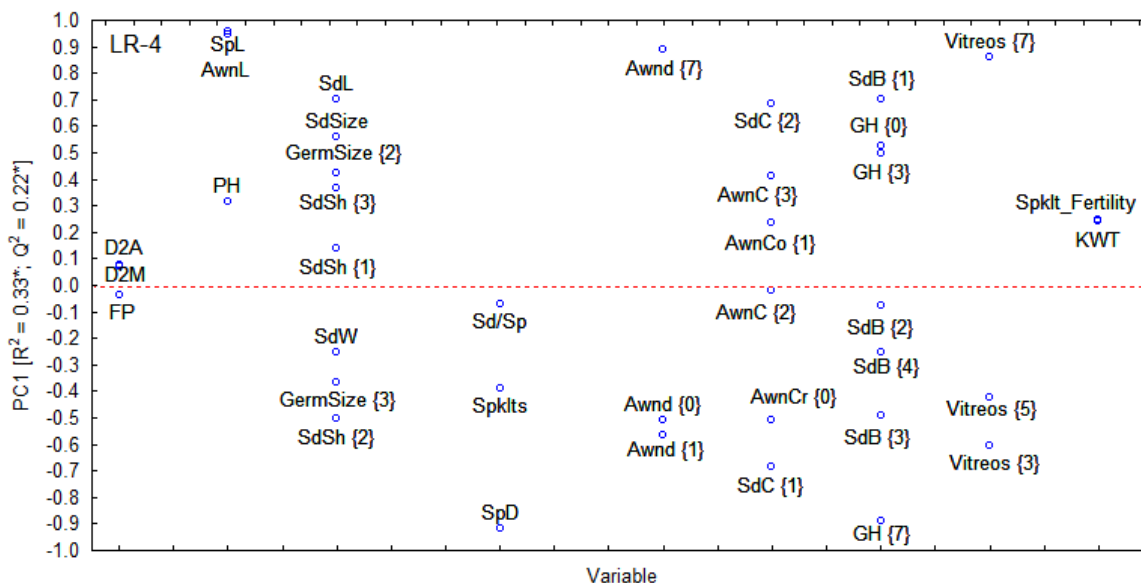


Figure 5. The first principal component (PC1) and coefficients of determination at the prediction (R2) and validation (Q2) phases of the PC model building derived from phenological, quantitative and qualitative traits in the first population (LR4) in a wheat landrace from Oman.

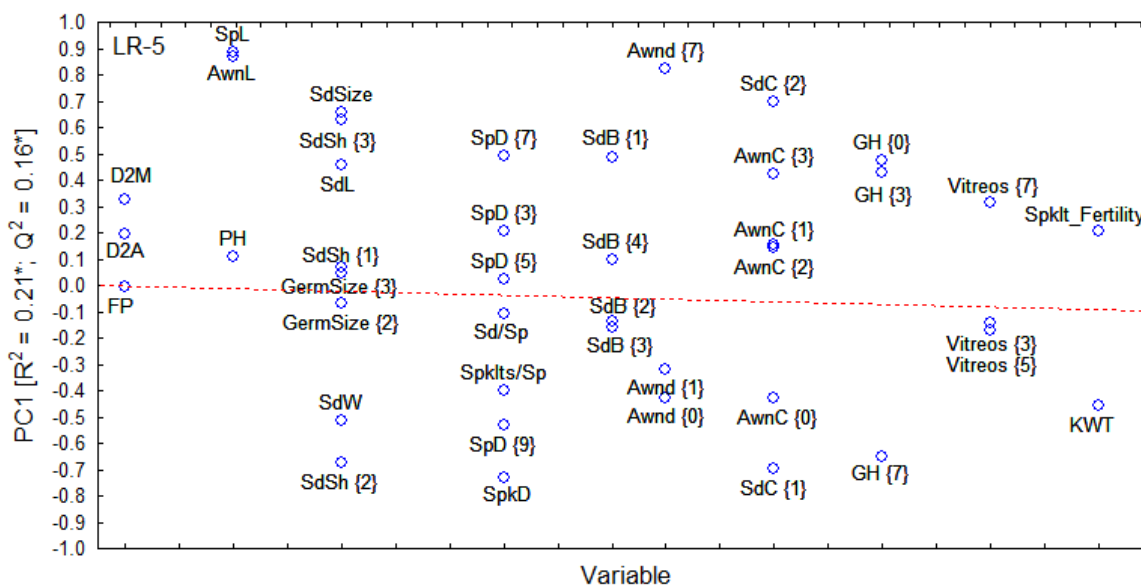


Figure 6. The first principal component (PC1) and coefficients of determination at the prediction (R2) and validation (Q2) phases of the PC model building derived from phenological, quantitative and qualitative traits in the first population (LR5) in a wheat landrace from Oman.

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 awnness, 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

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 glume hairiness variants as random factor) of phenological and quantitative variables in a wheat landrace from Oman.

Variable	Fixed factor		Random factor		
	<u>F-value</u>	<u>p-F</u>	<u>% variance</u>	<u>z-value</u>	<u>p-z</u>
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		
	<u>F-value</u>	<u>p-F</u>	<u>% variance</u>	<u>z-value</u>	<u>p-z</u>
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 awnness variants as random factor) of phenological and quantitative variables in a wheat landrace from Oman.

Variable	Fixed factor		Random factor		
	<u>F-value</u>	<u>p-F</u>	<u>% variance</u>	<u>z-value</u>	<u>p-z</u>
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		
	<u>F-value</u>	<u>p-F</u>	<u>% variance</u>	<u>z-value</u>	<u>p-z</u>
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 awnness 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 awnness 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		
	<i>F</i> -value	<i>p</i> - <i>F</i>	% variance	<i>z</i> -value	<i>p</i> - <i>z</i>
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		
	<u>F-value</u>	<u>p-F</u>	<u>% variance</u>	<u>z-value</u>	<u>p-z</u>
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 $\pm$ 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 $\pm$ 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
Awnness	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, H_t and population differentiation, G_{st}) 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}
Awnness	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 awnness 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.

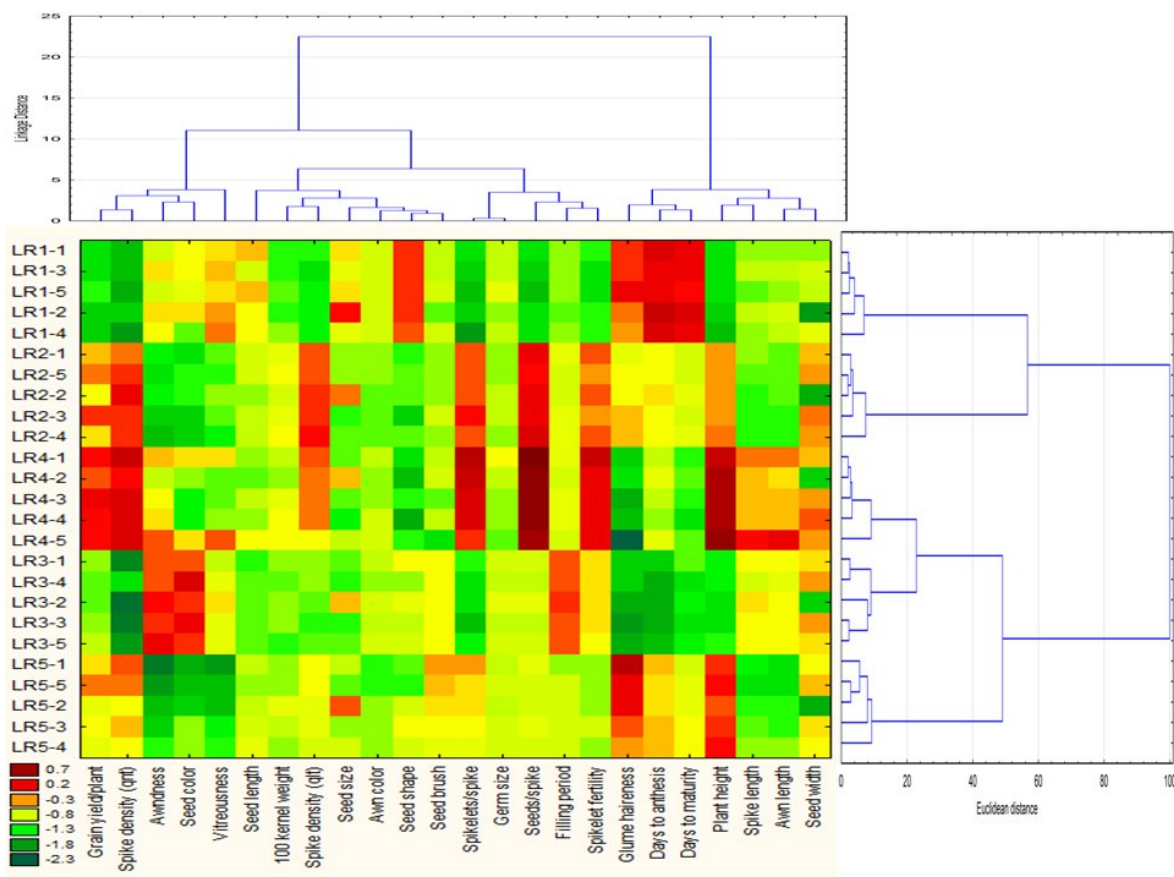


Figure 7. Hierarchical and joint cluster analyses of five sub-samples (-1 to -5) derived from each of five landrace populations (LR1 to LR5; Y-axis) and 24 standardized phenological, quantitative and qualitative traits measured or recorded on 800 plants of a wheat landrace from Oman.

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.

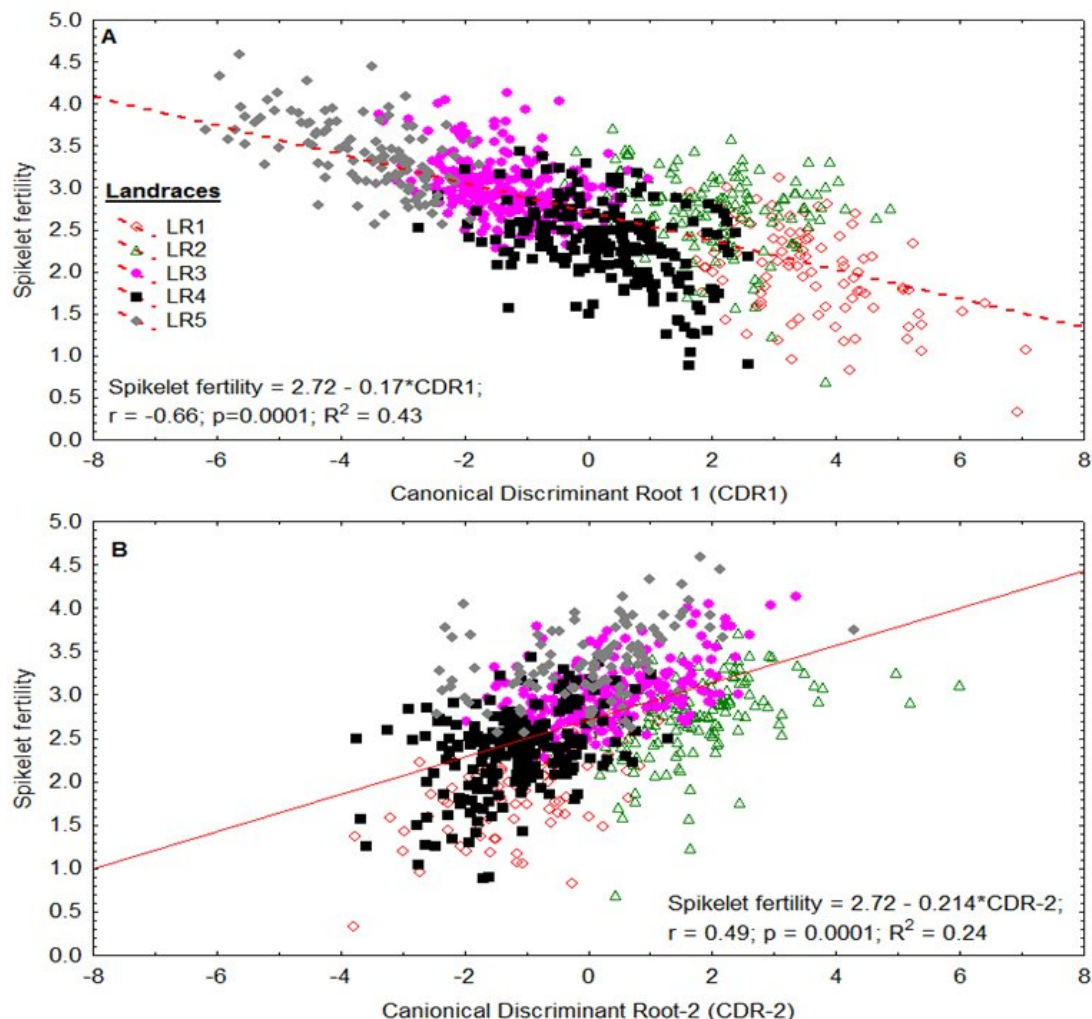


Figure 8. Linear relationships between spikelet fertility and each of the first canonical discriminant root, CDR-1, (A) and second CDR-2 (B) in five populations (LR1 to LR5) of a wheat landrace from Oman (See standardized coefficients in Table 3 for details).

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.

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	<i>0.07</i>	0.54	0.68	0.68	0.15	0.29
		Spike length	<i>0.05</i>	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	<i>0.11</i>	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	<i>0.04</i>
		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	
		Awnness	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	
		Spike density	0.94	0.99	0.00	0.90	0.69	0.69	
		Awnness	0.00	0.00	0.78	0.85	0.74	0.74	
	Variance		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	
		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
Color				Yield	0.08	0.74	0.56	-0.42	0.63
		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 in 1914 (*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, 2012). 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 ethno-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 quite 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 hierarchical 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 Zencirçi 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 qualitative 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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REGULAR ARTICLE

Wheat landraces from Oman: A botanical analysis

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Abstract

The wheat landraces of Oman are characterized. Their main constituents are *Triticum aestivum* L. ssp. *aestivum*, *T. aestivum* ssp. *hadropyrum* (Flaksb.) Tzvel., *T. compactum* Host, *T. aethiopicum* Jakubz. ssp. *aethiopicum*, *T. aethiopicum* ssp. *vavilovianum* Jakubz. et A. Filat. and *T. dicoccon* Schrank. The classification of the landraces was performed using the morphological method developed by Dorofeev, Filatenko et al. (1979), considering species, subspecies, convarieties and a great number of botanical varieties. Single landraces contained up to three different species ("Sareeaa") and up to 17 different botanical varieties ("Missani"). *T. aethiopicum* var. *hajirensis* A. Filat. et K. Hammer is newly described. Keys for the determination of important Omani wheat races are proposed. 15 wheat landraces of Oman are characterized morphologically. A detailed list describing origin, local names, and infraspecific taxa of the material is provided. Transformation processes of the oasis settlements lead to a replacement of the traditional agricultural systems and the landraces are threatened by genetic erosion. Additional measures are necessary to increase the possibilities for on-farm conservation of the valuable material of landraces.

Key words: Wheat, Landraces, *Triticum* sp., Oman, Morphological characterization, Botanical classification

Introduction

Oman on the Arabian Peninsula at the crossroads of inter-regional exchange including also cultivated plants (Gebauer et al., 2007; Hammer et al., 2007) is still rich in landraces of various crops. For a long time Oman was a closed country with first possibilities for botanical exploration, especially in the last century. Older reports about wheats are very limited (Schwarz, 1939; Mandeville, 1977). The presence of different wheat species was not clear. Only some reports from neighbouring Yemen (Flaksberger, 1935; Vavilov, 1931, 1964) allowed some conclusions. A note about wheat in Oman opened the way for new activities (Akhtar, 1981; Chapman, 1985). In the late 1980s Oman was included in worldwide activities for the collection of plant genetic resources (Guarino, 1990) and the first information about the still existing cultivation of *Triticum*

dicoccon appeared. At the beginning of the new millennium a program was started for exploring and collecting the wheat landraces of Oman reporting about wheat landraces from Hajir Mountains and describing new botanical varieties of hexaploid wheats (Al-Maskri et al., 2003). Hammer et al. (2004a) also found *T. dicoccon* subsp. *asiaticum* Vav. in Al Hamra, Misfat Abreen in the same Hajir Mountains.

Wheat (*Triticum* L.) is one of the most important staple foods in the world and its importance becomes even more acute as the global population increases. Thus, its characterization and application in breeding programs is very crucial. The wealth of the Omani landraces has been stressed in the last years (Filatenko et al., 2008).

The importance of landraces as an important basis for present and future breeding was recognized relatively late (von Proskowetz, 1890). Their possible loss by the introduction and spread of new highly productive varieties has been stressed also by Bauer (1914), Tschermack (1915) and Schindler (1918). Their preservation in genebanks was proposed, but it was not until the development of the "plant genetic resources movement" (Pistorius, 1997) that their value was adequately appreciated. Zeven (1998) provided the necessary definitions and classifications for

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landraces. He also questioned the on-farm activities, as they have been done formerly, for the maintaining of landraces (Zeven, 1996). Landraces are commonly genetically heterogeneous, developed through traditional agriculture over thousands of years by local farmers (Brush, 1999; Hammer and Diederichsen, 2009). Landraces have remained variable over long times, because eco-geographical structures are largely adaptive. Wheat farming in Oman is dependent on irrigation except for a small area in northern Oman which depends on rainfall.

Material and Methods

Exploration and collecting missions have been organized in Oman (Al Maskri et al., 2003; Al Khanjari et al., 2005). Samples have been transferred to the experimental fields of the University of Kassel in Witzenhausen where the characterization and evaluation of the material took place.

The description of agronomically important and useful characteristics is an important prerequisite for effective and efficient use of germplasm collections in future breeding programs.

The checklist-method has been used for a species survey (Hammer et al., 2004b, 2009).

For the characterization of the material, diversity studies have been carried out. Following the modern approach, a molecular evaluation was performed using microsatellites (Al Khanjari et al., 2005, 2007 a and b).

After a preliminary morphological characterization in 2002/ 2003 (Al Maskri et al., 2003; Hammer et al., 2004a), the classification and identification of the germplasm material was determined in 2010 (A. Filatenko). The basis for this work was the classical approach of Dorofeev, Filatenko et al. (1979) which allowed not only the determination of the species (for species designation we followed Hammer et al. (2011)), but also the infraspecific categories (a translation of the monograph is in preparation – Knüpffer et al., 2004). The methodology was developed in the Vavilov Insitute, St. Petersburg and proved to be useful for an exact classification of the material, for getting information towards its diversity and for following the process of genetic erosion (Bürkert et al., 2006), particularly in cases of monitoring landraces in certain areas (Hammer et al., 1996).

A map of Oman is presented in Figure 1, a photo of variable landrace is shown in Figure 2, and the main collecting areas are presented in Table 1.

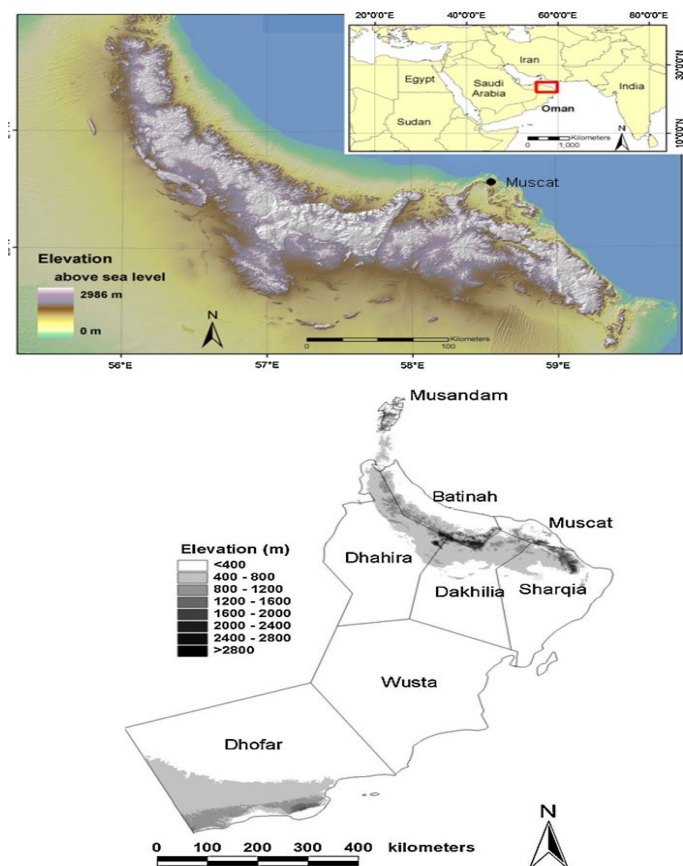


Figure 1. Map of Oman showing the Hajar Mountains where most of the newly discovered botanical wheat varieties were found (above) and the country's different districts where the wheat germplasm survey was conducted (below)



Figure 2. Typical spikes of the landrace „Walidi“ from Baladseet (Biladsayt) (left),
T. compactum var. *maqtaense* (A. Filat. et K. Hammer) A. Filat. (Walidi) (right).

Table 1. Summary of the collection areas (point range).

District	Altitude	Latitude	Longitude
Dhahira	300m - 700m	56°30 - 56°37	23°41 - 23°18
Batinah	400m - 800m	56°29 - 57°37	23°59 - 23°11
Dakhilia	300m - 900m	57°04 - 57°12	22°48 - 23°06
Sharquia	300m - 1500m	59°09 - 58°45	22°59 - 23°47
Musandam	50m - 400m	55°57 - 56°18	26°04 - 24°24

Results and Discussion

Many botanical varieties of cultivated wheat have been observed and collected in Oman. The results of the classification are shown in Appendix 1. A short discussion arranged by species is provided in the following. Wild-growing species of wheat and *T. monococcum* L. have not been found in Oman.

Hexaploid wheats

Triticum compactum Host

The finding of a wide distribution of *T. compactum* in Oman is especially interesting. In the neighbouring countries this species is very rare (Iran), or not found at all (Ethiopia).

It is ecologically a typical mountain wheat, which includes, according to Vavilov (1935), moisture-loving forms with a low temperature requirement in the period of ripening and tolerance against decreasing temperature in spring, which are not demanding with respect to soil and cultivation conditions.

Three groups of varieties are distinguished within *T. compactum*. These were: convar.

compactum, convar. *rigidicompactum* (Kudr.) A. Filat. and convar. *inflatum* (Vav. et Kob.) A. Filat. The latter one was not found in Oman (see Al Khanjari, 2005, 2007b, 2008).

Plants and spikes of *T. compactum* are of delicate structure, glumes usually thinly coriaceous, with a transverse depression at the base. Caryopses loosely enclosed by lemma and palea and easy to thresh. Convar. *compactum* is distributed throughout the whole Old World. In the 20th century it was particularly cultivated in Siberia, Russian Far East, Yakutia, Mongolia and China but never common.

T. compactum is not associated with any particular distribution area, but, according to Vavilov (1964), it represents relicts to a considerable degree. Two botanical varieties belong to convar. *compactum*, namely, var. *balatseetense* (K. Hammer et A. Filat.) A. Filat., var. *maqtaense* (A. Filat. et K. Hammer) A. Filat.

Spikes of this group are awned, half-awned; less often awnless, glumes rigid, more often half-rigid; caryopses closely enclosed in lemma and

palea, but are usually easy-to-thresh, less often threshing is difficult.

Geographical distribution

Mountain and foothill zones of Middle and South-West Asia, Transcaucasia, Mongolia, Oman.

Four botanical varieties belong to convar. *rigidicompactum*: var. *muticulinaza* Kudr., var. *linaza* Koern., var. *sedabense* A. Filat. et K. Hammer, var. *omanense* A. Filat et K. Hammer.

Spikes of this group are awned, semi-awned or sometimes awnless, glumes rigid or usually semi-rigid; caryopses closely enclosed by lemma and palea, usually easy or sometimes difficult to thresh.

Generally, convar. *rigidicompactum* is characterised by a distinct polymorphism and represented by a considerable number of varieties.

Triticum aestivum L.

From the typical common wheat in Oman *T. aestivum* subsp. *aestivum* (European wheat) and *T. aestivum* subsp. *hadropyrum* (Asiatic wheat) convar. *semirigidum* A. Filat. et Dorof. are present.

Spikes of convar. *semirigidum* awned or awnless, semi-robust; glumes less coarse than those of convar. *rigidum*, with less distinct venation, caryopses not so firmly enclosed by palea and lemma, not falling, but easy to thresh.

Geographical distribution. *T. aestivum* convar. *semirigidum* has a very wide geographical distribution: West Asia, India, China, Mediterranean, Lower Volga, Transcaucasia and Arabian Peninsula (Oman).

Out of the 59 described varieties (Dorofeev, Filatenko et al., 1979) of convar. *semirigidum*, 12 were collected in Oman (only subconvar. *semirigidum*), one of them is a new variety (bold face): var. *barbarossa* (Alef.) Mansf., var. *graecum* (Koern.) Mansf., var. *hostianum* (Clem.) Mansf., var. *ibraense* K. Hammer et A. Filat., var. *insigne* (Kudr.) A. Filat., var. *leucospermum* (Koern.) Mansf., var. *meridionale* (Koern.) Mansf., var. *pseudoerythrospermum* (Kudr.) A. Filat., var. *pseudohostianum* (Flaksb.) Mansf., var. *pseudoleucospermum* (Kob.) Mansf., var. *pseudopyrothrix* (Kob.) Mansf., var. *pulchrum* (Kudr.) A. Filat.

Subsp. *aestivum* – European subspecies is present with 7 varieties in Oman; the altitudinal distribution ranged **between** 50 - 1500 m above sea level.

Plants and spikes of this group are of delicate structure, glumes usually thinly coriaceous, very various in shape, with a transverse depression at the base. Caryopses loosely enclosed by lemma and palea, easy to thresh, many forms with easily

shedding grains exist, the degree of enclosure of the caryopsis by the lemma and palea is determined by the amount of convexity of the lower half of the glume and not by the coarse texture of the glume as in subsp. *hadropyrum*.

Geographical distribution. Throughout the range of *T. aestivum*.

Out of the 38 listed varieties of subsp. *aestivum* (Dorofeev, Filatenko et al., 1979), 3 were found in Oman: var. *aestivum*, var. *anglicum* (Aschers. et Graebn.) A. Filat., var. *lutescens* (Alef.) Mansf. and 3 have been newly discovered by us: var. *arabicum* K. Hammer et A. Filat., var. *pseudosoharicum* K. Hammer et A. Filat., var. *soharicum* K. Hammer et A. Filat.

The botanical diversity of hexaploid wheat species is poorer than in the main center of their origin – Southwest Asia (Turkistan, Afghanistan, East Iran, Northwest India). But, the botanical composition of the hexaploid wheats and the newly found varieties are good indications of the long-time evolution in the territories of Oman.

Tetraploid wheats

Triticum dicoccon Schrank

Full description about the hulled tetraploid *T. dicoccon* is available in Hammer et al. (2004a). *T. dicoccon* from Oman is intermediate between Asiatic (ssp. *asiaticum* Vav.) and Ethiopian (ssp. *abyssinicum* Vav.) races. It has not yet been included in molecular studies (Zhang et al., 2006; Teklu et al., 2007). In recent years it has become very rare. A last sample of aged seeds with no germinability has been found by the authors in 2006 in an Omani seed store (Gebauer et al. 2007).

The tetraploid naked wheats of Oman are also very interesting; they are very similar to Ethiopian tetraploids and belong to *T. aethiopicum* Jakubz. Earlier, this species was considered endemic to Ethiopia and Yemen. New material was also found in Egypt recently (Gowayed, 2009). The history and evolution of this species have to be revised on the basis of the new findings (Sinskaja, 1969; see also Filatenko et al., 2003).

Vavilov (1931) first distinguished the Ethiopian naked tetraploid wheats as separate subspecies within the species *T. durum* and *T. turgidum*. Percival (1921) had previously included the Ethiopian wheat in *T. dicoccon* on the basis of their similar number of vascular bundles in the coleoptile. Later Vavilov (1964) emphasised the peculiarity of the Ethiopian tetraploid naked wheats (presence of violet-seeded forms, and on the basis of the number of vascular bundles in the coleoptile). Ethiopian wheat is similar to *T.*

aestivum in the characters of the spike, the diversity of the glumes, the presence of awnless, semi-awned and inflated forms and the scabridity of the leaf blades. Some of its dense-spiked forms resemble compact forms of *T. aestivum*/*T. compactum*. The resemblance to the tetraploid *T. carthlicum* Nevski is shown in the development of awns on the glumes, the thin spike rachis (not as thin, however, as that of *T. carthlicum*) and the rugose (wrinkled) dorsal side of the caryopsis. The presence of forms with a well-developed glume keel, with two clearly distinct rows on the lateral side of the spike and with a solid culm show that the Ethiopian wheats as close to *T. durum* Desf. On the basis of the latter resemblance, as well as on their tetraploid nature, Vavilov (1931) referred them to *T. durum* subsp. *abyssinicum* Vav. (see Hanelt and IPK, 2001) and emphasised, in so doing, their clear distinction from the common types of *T. durum* and *T. aestivum*.

Turgidoid Ethiopian wheats, previously assigned to *T. turgidum* subsp. *abyssinicum* Vav., resemble *T. turgidum* L. in characters of the glume (shorter than lemma; inflated) and the caryopsis (gibbous). However, Vavilov (1931) noted that the Mediterranean *T. turgidum* was sharply distinct from the turgidoid Ethiopian wheats and pointed out the greater ecological and morphological similarities of all groups of Ethiopian wheats. Vavilov considered the presence of characters of *T. aestivum*, *T. durum* and *T. turgidum* in *T. aethiopicum* as a feature of the primitiveness of their cultivation, although it may be very ancient.

Flaksberger (1939) confirmed the repeated statements by Vavilov of the need to distinguish the Ethiopian wheat as an independent species. Moreover, he considered this wheat to have a complex of characters providing arguments for raising it to species rank as *T. abyssinicum* (a later homonym). In 1947 Jakubziner renamed this species - *T. aethiopicum* (Dorofeev, Filatenko et al., 1979).

This species was divided by A. Filatenko into three subspecies: 1) subsp. *aethiopicum* (shows similarity to *T. aestivum* and *T. carthlicum*); 2) subsp. *vavilovianum* Jakubz. et A. Filat. (has characters of *T. durum*); 3) subsp. *turgidoides* A. Filat. (see Dorofeev et al., 1979). We have discovered in Oman only the varieties of *T. aethiopicum* subsp. *aethiopicum* and subsp.

vavilovianum. Subsp. *turgidoides* is very rare as a crop in Ethiopia now. S. Cleuziou and L. Costantini (1980) indicate the prehistoric finding of *T. turgidum* in Oman. But it could be rather *T.*

aethiopicum subsp. *turgidoides*, somewhat similar in grain shape to *T. turgidum*. Moreover, in Oman there were never good conditions for the cultivation of *T. turgidum*.

***T. aethiopicum* Jakubz. subsp. *aethiopicum*.**

Spikes are typically 6–12 cm long, lax (D about 17), mostly spindle-shaped, oval in cross-section, awned or awnless. Glumes smooth (shiny or with a slight wax bloom) or pubescent, with an awn (up to 7 cm long) or with acute keel tooth. Awns thin, long, slightly divergent, almost parallel to the spike rachis. Caryopsis narrow, elongated, slightly rugose (wrinkled), more or less flat on the ventral side, usually violet, less often red and rarely white. In Ethiopia cultivated at 2400–3000 m.

For the first time the var. *rarissimum* (Vav.) A. Filat. was found in Wadi Bani Khalid in the Sharqia province of Oman at 300–1500 m. Later on, additional races were collected: var. *pseudorarum* (Vav.) A. Filat., var. *uncinatum* (Perciv.) A. Filat., var. *amharicum* (Perciv.) A. Filat.

The majority of tetraploid naked wheats of Oman belong to *T. aethiopicum* subsp. *vavilovianum*.

***T. aethiopicum* subsp. *vavilovianum* Jakubz. et A. Filat.** – Vavilov's subspecies (description after Dorofeev et al., 1979)

Spikes are medium sized to short (5–9 cm long), moderately dense (D=30–40) or dense (D=40–59), elongated, cylindrical or sometimes pyramidal. Glumes glabrous (shiny or with wax bloom) or pubescent, of various shapes and sizes, delicate or rather coarse in consistency; keel clearly distinct, but comparatively narrow, reaching the base of glume, base without transverse depression and not longitudinally wrinkled. Keel tooth acute, short to awn-like (up to 7 cm long). Caryopses short, orbicular, quite often with hump on dorsal side, white, red or violet. Tuft sparse (stems 2–3), with a small number of subsidiary spikes. Plants quite short. Culm thin, flexible, solid or with a small hollow. Sheath slightly pubescent. Leaf blades scabrous.

Subsp. *vavilovianum* is divided into two convarieties.

Key for the determination of the convarieties of *T. aethiopicum* subsp. *vavilovianum* Jakubz. et A. Filat. (key translated from Dorofeev, Filatenko et al. 1979)

1. Spikes cylindrical, 5–9 cm long, dense (D=30–40) convar. ***vavilovianum*** A. Filat.

+ Spikes narrowed towards the apex, up to 5 cm long, dense (D>40) convar. ***compactum*** (Vav.) A. Filat.

The most part of varieties in Oman belongs to convar. *vavilovianum*, less to convar. *compactum*.

Convar. *vavilovianum* – group of dense-spiked varieties.

Out of the 34 described varieties of convar. *vavilovianum*, 11 were discovered in Oman: var. *bialbum* (Vav.) A. Filat., var. *bicolor* (Chiov.) A. Filat., var. *comitans* (Vav.) A. Filat., var.

densimenelikii (Vav.) A. Filat., var. *mahsanense* A. Filat. et K. Hammer (Filatenko et al. 2010), var. *pilosinigrum* (Vav.) A. Filat. (Al Khanjari et al. 2008), var. *pseudorubripubescens* (Vav.) A. Filat., var. *pseudotomentosum* (Perciv.) A. Filat., var. *tchetchericum* (Vav.) A. Filat., var. *tomentosum* (Perciv.) A. Filat. var. *hajireense* A. Filat. et K. Hammer is described below.

Key for the determination of varieties of convar. *vavilovianum* A. Filat. of Oman.

Glumes						Awns		Variety
white	white with black margin	red	red with black margin	black on background		same as glumes	black	
				white	red			
<i>Spikes awned</i>								
<i>Spikes glabrous</i>								
<i>Caryopses red</i>								
+	—	—	—	—	—	+	—	<i>densimenelikii</i>
—	—	—	—	+	—	—	+	<i>bicolor</i>
<i>Caryopses white</i>								
+	—	—	—	—	—	+	—	<i>bialbum</i>
<i>Spikes pubescent</i>								
<i>Caryopses red</i>								
+	—	—	—	—	—	+	—	<i>tchertchericum</i>
+	—	—	—	—	—	—	+	<i>comitans</i>
—	—	+	—	—	—	—	+	<i>pseudorubripubescens</i>
—	—	—	—	—	+	—	+	<i>pilosinigrum</i>
—	—	—	—	+	—	—	+	<i>mahsanense</i>
<i>Caryopses white</i>								
+	—	—	—	—	—	+	—	<i>tomentosum</i>
+	—	—	—	—	—	—	+	<i>pseudotomentosum</i>
<i>Spikes half-awned (Spikes pubescent)</i>								
<i>Caryopses white</i>								
—	—	—	+	—	—	—	+	<i>hajirensae</i>

T. aethiopicum convar. *vavilovianum* var. *hajireense* A. Filat. et K. Hammer, **var. nova**

– Spica rubra marginibus glumarum nigris.

Typus: Peninsula Arabica, Oman, cultivar localis Sareeaa, exped. № 270-3b, districtus Musandam, prope pagus Lkasab, a supra mare 300 m. 2001, leg. S. Alkhanjari and K. Hammer. Herbarium:GAT

Convar. **compactum** A. Filat. – group of extremely dense-spiked varieties.

Out of the 19 described varieties of convar. *compactum*, 3 were discovered in Oman: var.

pseudoarabicum (Vav.) A. Filat., var. *nubicum* (Vav.) A. Filat., var. *ptolomaeum* (Vav.) A. Filat.

Key for the determination of the varieties of *T. aethiopicum* convar. *compactum* (Vav.) A.Filat. in Oman

Glumes						Awns		Variety
white	white with black margin	red	red with black margin	black on background		same as glumes	black	
				white	red			
Spikes glabrous								
Caryopses red								
+	—	—	—	—	—	+	—	ptolomaeum
Spikes pubescent								
Caryopses red								
+	—	—	—	—	—	—	+	pseudoarabicum
Caryopses white								
+	—	—	—	—	—	—	+	nubicum

Among tetraploid accessions some were similar to *T. durum* Desf. (Al Maskri et al., 2003; Al Khanjari et al., 2005). But these forms have a spike more soft and tender, than that of *T. durum*, the culm filling is weak or intermediate in upper internode as with *T. aethiopicum*. Some former determinations could not be confirmed by a new classification done in 2010.

The rich and unique naked hexaploid and tetraploid wheats of Oman testify that wheat is not a casual and recent component of cultural flora of this country, but has an old history of cultivation. Ancient traces of agriculture are found in Arabia in the 3rd millenium BC. The oases of Oman were, at that time, early settlements where early farmers cultivated date palms and sowed distichous and polystichous barley, wheat, sorghum and jujube (Cleuziou and Costantini, 1980). Oman was the important staging post on crossing trade routes

which connected Mesopotamia, Persia, the Indus valley and Africa (Shnirelman, 1989).

A wide variation was observed in Dahirah region where cultivated fields were large in size. Batinah region is the second largest in size and number of the fields. Although Batinah is known to have many fields, most fields have been affected by salinity. Sharqia region is spread over a large area but there are few landraces. Farmers in the area cultivate a special type of wheat locally called “Walidi”. The Dakhilia region is the smallest region in size with small fields as well. Important landraces and their morphological constituents are shown in Table 2; where a large level of variation can be seen within this region.

In total 29.49% of the local landraces (as expressed by their botanical varieties) have not been reported elsewhere in the world.

Table 2. Important landraces from Oman and their constituents (species and botanical varieties).

Landrace	Species	Botanical varieties
„Missani“	<i>T. aestivum</i>	var. <i>aestivum</i> , var. <i>anglicum</i> , var. <i>arabicum</i> , var. var. <i>barbarossa</i> , var. <i>hostianum</i> , var. <i>oblivense</i> , var. var. <i>pseudohostianum</i> , var. <i>soharicum</i> .
	<i>T.aethiopicum</i>	var. <i>amharicum</i> , var. <i>comitans</i> , var. <i>densimenelikii</i> , var. <i>mahsanense</i> , var. <i>pseudorarum</i> , var. <i>pseudorubropubescens</i>
„Buwaidha“	<i>T. aestivum</i>	var. <i>ptolomaeum</i> , var. <i>tchertchericum</i> , var. <i>uncinatum</i> , var. <i>soharicum</i>
	<i>T.aethiopicum</i>	var. <i>comitans</i> , var. <i>densimenelikii</i> , var. <i>uncinatum</i>
„Sareea“	<i>T. aestivum</i>	var. <i>graecum</i> , var. <i>ibraense</i> , var. <i>pseudoerythroleucon</i>
	<i>T. compactum</i>	var. <i>baladseetense</i> , var. <i>sedabense</i>
	<i>T.aethiopicum</i>	var. <i>densimenelikii</i>
„Malki“	<i>T.aethiopicum</i>	var. <i>pseudorarum</i>

Table 2. Contd..

Landrace	Species	Botanical varieties
„Sareeaa“ – „Bulwaidha alwadi“	<i>T. aethiopicum</i>	var. <i>densimenelikii</i>
„Cooley“	<i>T. aestivum</i>	var. <i>insigne</i> , var. <i>ibraense</i> , var. <i>lutesecens</i> , var. var. <i>pseudohostianum</i> , var. <i>leucospermum</i> , var. <i>meridionale</i> , var. <i>hostianum</i>
	<i>T. compactum</i>	var. <i>baladseetense</i> , var. <i>muticilinaza</i> , var. <i>omanense</i> , var. <i>linaza</i>
„Walidi“	<i>T. aestivum</i>	var. var. <i>aestivum</i> , var. <i>hostianum</i> , var. <i>leucospermum</i> , var. <i>pseudoleucospermum</i> , var. <i>pulchrum</i> , var. <i>soharicum</i>
	<i>T. compactum</i>	var. var. <i>baladseetense</i> , var. <i>densimenelikii</i> , vv var. <i>maqtaense</i> , var. <i>muticilinaza</i>
„Hamira“	<i>T. aestivum</i>	var. var. <i>aestivum</i> , var. <i>hostianum</i> , var. <i>ibraense</i> , var. var. <i>pseudoerythrospermum</i> , var. <i>pseudohostianum</i> , var. <i>pseudovelutinum</i> , var. <i>soharicum</i>
	<i>T. compactum</i>	var. var. <i>baladseetense</i>
„Greda“	<i>T. aestivum</i>	var. var. <i>graecum</i>
„Shalut“	<i>T. aestivum</i>	var. var. <i>aestivum</i> , var. <i>hostianum</i> , var. var. <i>pseudoerythrospermum</i> , var. <i>soharicum</i> , var. var. <i>pseudopyrothrix</i> , var. <i>pseudodovelutinum</i>
	<i>T. compactum</i>	var. var. <i>pulchrum</i>
„Shawie“	<i>T. aestivum</i>	var. var. <i>muticilinaza</i>
„Khatie“	<i>T. aestivum</i>	var. var. <i>soharicum</i>
„Grada“	<i>T. aestivum</i>	var. var. <i>hostianum</i> , var. <i>ibraenese</i> , var. <i>pseudovelutinum</i> , var. var. <i>leucospermum</i> , var. <i>pulchrum</i>
„Musfsikha“	<i>T. aestivum</i>	var. var. <i>hostianum</i>

Conclusions

Various morphological variations in wheat landraces were found in Oman. Most of the fields were mixed with other cereal crops. Approximately 90% of the wheat fields which were visited contained *Avena sativa* L., and approximately 10–20% contained *Hordeum vulgare* L. These findings confirm earlier reports by Al-Maskri et al. (2003). But a steep decline in the presence of wheat landraces, as already observed by Anon. (2000), has to be confirmed. The speed of transformation processes in the agriculture of oasis settlements of Oman is extremely high (Buerkert et al., 2007; Buerkert and Schlecht, 2010; Gebauer et al., 2010). Many of the small terraces (from 2 to 100 m²; Al-Maskri et al., 2003) have been abandoned. Programs for on-farm conservation of wheat and other genetic resources are urgently needed.

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Appendix 1. Botanical classification of Oman wheat (A.A.Filatenko, Gatersleben, 2010)

OMTRI	Probe N	Species	subspecies	convar.	subconvar.	varieties	Cultivar localis	Location	Region	District
21	180-4	<i>T. aestivum</i> L.	<i>aestivum</i>			<i>soharicum</i> K.Hammer et A. Filat.	Missani	Al Gum	Sur	Sharquia
22	180-4	<i>T. aestivum</i>	<i>aestivum</i>			<i>arabicum</i> K.Hammer et A. Filat.	Missani	Al Gum	Sur	Sharquia
31	104-1	<i>T. aethiopicum</i> Jakubz.	<i>aethiopicum</i>			<i>pseudororum</i> , <i>pseudorubripubescens</i>	Missani	Wadi Sermi Khabura	Khabura	Batinah
32	104-2	<i>T. aethiopicum</i>	<i>aethiopicum</i>			<i>pseudororum</i> (Vav.)A. Filat.	Missani	Wadi Sermi Khabura	Khabura	
33	104-4	<i>T. aethiopicum</i>	<i>aethiopicum</i>			<i>uncinatum</i> (Perciv.)A. Filat.	Buwaidha	Wadi Sermi Khabura	Khabura	Batinah
34	104-5	<i>T. aethiopicum</i>	<i>aethiopicum</i>			<i>uncinatum</i> (Perciv.)A. Filat.	Missani	Wadi Sermi Khabura	Khabura	Batinah
35	104-6-1	<i>T. aethiopicum</i>	<i>vavilovianum</i> Jakubz. et A. Filat.	<i>vavilovianum</i> A. Filat.		<i>comitans</i> (Vav.)A. Filat.	Missani	Wadi Sermi Khabura	Khabura	Batinah
36	104-6-2	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A. Filat.	Missani	Wadi Sermi Khabura	Khabura	Batinah
37	106-1	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A. Filat.	Missani	Al Zam	Rustaq	Batinah
38	106-2	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A. Filat.	Missani	Al Zam	Rustaq	Batinah
39	106-3	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>densimenelikii</i> (Vav.)A. Filat.	Sareea	Al Zam	Rustaq	Batinah
40	107-1	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A. Filat.	Missani	Al Mahsan	Wadi Bani Kharus	Batinah
41	107-2	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A. Filat.	Missani	Al Mahsan	Wadi Bani Kharus	Batinah
42	107-3	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A. Filat.	Missani	Al Mahsan	Wadi Bani Kharus	Batinah
43	107-5	<i>T. aethiopicum</i>	<i>aethiopicum</i>			<i>uncinatum</i> (Perciv.)A. Filat.	Missani	Al Mahsan	Wadi Bani Kharus	Batinah
44	109-5	<i>T. aethiopicum</i>	<i>aethiopicum</i>			<i>pseudororum</i> (Vav.)A. Filat.	Missani	Wadi Hibi - Al Hajal	Sohar	Batinah
45	109-6	<i>T. aethiopicum</i>	<i>aethiopicum</i>			<i>amharicum</i> (Perciv.)A. Filat.	Missani	Wadi Hibi - Al Hajal	Sohar	Batinah
45-1	109-6	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A. Filat.	Missani	Wadi Hibi - Al Hajal	Sohar	Batinah
46	111-3	<i>T. aestivum</i>	<i>hadropyrum</i> (Flaksb.) Tzvel.	<i>semirigidum</i> A. Filat. et Dorof.	<i>semirigidum</i> A. Filat. et Dorof.	<i>hostianum</i> (Clem.)Mansf.	Missani	Wadi Ahan	Sohar	Batinah
47	111-5	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>tchertchericum</i> , <i>comitans</i>	Missani	Wadi Ahan	Sohar	Batinah
48	112-10	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>tchertchericum</i> (Vav.)A. Filat.	Missani	Wadi Ahan	Sohar	Batinah
49	112-3	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>tchertchericum</i> , <i>comitans</i>	Buwaidha	Wadi Ahan	Sohar	Batinah
50	113-4-1	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A. Filat.	Missani	Wadi Ahan	Sohar	Batinah
51	113-4-2	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A. Filat.	Missani	Wadi Ahan	Sohar	Batinah
52	113-4-3	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A. Filat.	Missani	Wadi Ahan	Sohar	Batinah

53	120-1	<i>T. aethiopicum</i>	<i>aethiopicum</i>			<i>pseudorarum</i> (Vav.)A. Filat.	Malki	Al Raky	Wadi Bani Khalid	Sharquia
54	120-6-2	<i>T. aethiopicum</i>	<i>aethiopicum</i>			<i>pseudorarum</i> (Vav.)A. Filat.	Malki	Al Raky	Wadi Bani Khalid	Sharquia
55	120-9	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>mahsanense</i> A. Filat. et K. Hammer	Missani	Al Raky	Wadi Bani Khalid	Sharquia
56	126-7	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Buwaidha alwadi	Salma	Dhang	Dhahira
57	127-4	<i>T. aestivum</i>	<i>aestivum</i>			<i>aestivum</i>	Missani	Falaj Sudairen	Yanqul	Dhahira
58	128-1-1	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>densimenelikii</i> (Vav.)A.Filat.	Sareeaa	Bahla	Bahla	Dakhilia
59	131-1	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>densimenelikii</i> (Vav.)A.Filat.	Sareeaa	Gemat Barut	Bahla	Dakhilia
60	131-2	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>densimenelikii</i> (Vav.)A.Filat.	Sareeaa	Gemat Barut	Bahla	Dakhilia
61	132-1-1	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>compactum</i> (Vav.) A.Filat.		<i>ptolomaeum</i> (Vav.)A.Filat.	Missani	Seent Jabl Kuor	Bahla	Dakhilia
62	132-1-2	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>densimenelikii</i> (Vav.)A.Filat.	Missani	Seent Jabl Kuor	Bahla	Dakhilia
63	132-2	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>densimenelikii</i> (Vav.)A.Filat.	Sareeaa	Seent Jabl Kuor	Bahla	Dakhilia
64	132-3	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>densimenelikii</i> (Vav.)A.Filat.	Sareeaa-Buwaidha alwadi	Seent Jabl Kuor	Bahla	Dakhilia
65	138-1	<i>T. aethiopicum</i>	<i>aethiopicum</i>			<i>amharicum</i> (Perciv.)A.Filat.	Missani	Al Raky	Wadi Bani Khalid	Sharquia
66	138-2	<i>T. aethiopicum</i>	<i>aethiopicum</i>			<i>amharicum</i> (Perciv.)A.Filat.	Missani	Al Raky	Wadi Bani Khalid	Sharquia
67	138-4	<i>T. aethiopicum</i>	<i>aethiopicum</i>			<i>amharicum</i> (Perciv.)A.Filat.	Missani	Al Raky	Wadi Bani Khalid	Sharquia
68	140-12-1	<i>T. aestivum</i>	<i>aestivum</i>			<i>anglicum</i> (Aschers. Et Graebn.)A.Filat.	Missani	Falaj Sudairen	Yanqul	Dhahira
69	140-13-1	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>densimenelikii</i> (Vav.)A.Filat.	Sareeaa	Falaj Sudairen	Yanqul	Dhahira
70	140-13-2	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>densimenelikii</i> (Vav.)A.Filat.	Missani - Buwaidha	Falaj Sudairen	Yanqul	Dhahira
71	140-25	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>densimenelikii</i> (Vav.)A.Filat.	Missani	Falaj Sudairen	Yanqul	Dhahira
72	150-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Sareeaa	Wadi Ahan	Ibri	Dhahira
73	150-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Sareeaa	Wadi Ahan	Ibri	Dhahira
74	150-4	<i>T. compactum</i>		<i>rigidcompactum</i>	<i>rigidcompactum</i>	<i>balatseetense</i> (Hm. et Filat.) A. Filat.	Sareeaa	Wadi Ahan	Ibri	Dhahira
75	190-5	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans, pseudorubripubescens</i>	Missani Arabic	Kasab	Kasab	Musandam
75-1	190-5	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>barbarossa</i> (Alef.)Mansf.	Missani Arabic	Kasab	Kasab	Musandam
76	190-3	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A.Filat.	Missani	Kasab	Kasab	Musandam
77	190-4	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A.Filat.	Missani	Kasab	Kasab	Musandam
78	190-6	<i>T. aethiopicum</i>	<i>aethiopicum</i>			<i>amharicum</i> (Perciv.)A.Filat.	Missani	Kasab	Kasab	Musandam
79-1	190-7	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudohostianum, hostianum</i>	Missani Arabic	Qaa	Kasab	Musandam
79	190-7	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A.Filat.	Missani Arabic	Qaa	Kasab	Musandam
80	190-8	<i>T. aestivum</i>	<i>aestivum</i>			<i>oblivense</i> (Greb.) A. Filat.	Missani	Ras Auqab	Kasab	Musandam

81	270-3	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>comitans</i> (Vav.)A.Filat.	Missani	Lima	Lima	Musandam
82-1	270-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudohostianum</i> (Flaksb.) Mansf.	Missani	Lima	Lima	Musandam
82	270-2	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>tchertchericum</i> (Vav.)A. Filat.	Missani	Lima	Lima	Musandam
87	107-4	<i>T. compactum</i> Host		<i>rigidcompactum</i> (Kudr.) Dorof. et A.Filat.	<i>rigidcompactum</i> A.Filat. et Dorof.	<i>muticilinaza</i> Kudr.	Cooley	Al Mahsan	Wadi Bani Kharus	Batinah
88	109-1	<i>T. compactum</i>		<i>compactum</i>		<i>baladseetense</i> (Hm. et A. Filat.) Filat.	Cooley	Wadi Hibi - Al Haja	Sohar	Batinah
89	109-2	<i>T. compactum</i>		<i>rigidcompactum</i>	<i>rigidcompactum</i>	<i>muticilinaza</i> Kudr.	Walidi	Wadi Hibi - Al Haja	Sohar	Batinah
89-1	109-2-6	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Walidi	Wadi Hibi - Al Haja	Sohar	Batinah
90	109-3	<i>T.aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K.Hammer et A. Filat.	Hamira	Wadi Hibi - Al Haja	Sohar	Batinah
91	109-10	<i>T.aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K.Hammer et A. Filat.	Walidi	Wadi Hibi - Al Haja	Sohar	Batinah
92	111-1	<i>T.aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>graecum</i> (Koern.) Mansf.	Greda	Wadi Ahan	Sohar	Batinah
93	111-4	<i>T.aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Walidi	Wadi Ahan	Sohar	Batinah
94	111-6	<i>T. compactum</i>				<i>linaza</i> Koern.	Cooley	Wadi Ahan	Sohar	Batinah
95	111-7	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Cooley	Wadi Ahan	Sohar	Batinah
96	111-8-1	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Shalut	Wadi Ahan	Sohar	Batinah
97	111-8-2	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Shalut	Wadi Ahan	Sohar	Batinah
98	111-9	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Hamira	Wadi Ahan	Sohar	Batinah
99	111-10(112-11)	<i>T. compactum</i>		<i>compactum</i>		<i>baladseetense</i> (Hm. et Filat.)A. Filat.	Hamira	Wadi Ahan	Sohar	Batinah
100	112-1	<i>T. compactum</i>		<i>compactum</i>		<i>maqtaense</i> A. Filat. et Hammer	Walidi	Wadi Ahan	Sohar	Batinah
101	113-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Cooley	Wadi Ahan	Sohar	Batinah
102	113-10	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoerythrospermum</i> (Kudr.) A.Filat.	Cooley	Wadi Ahan	Sohar	Batinah
103	113-11	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pulchrum</i> (Kudr.) A. Filat.	Walidi	Wadi Ahan	Sohar	Batinah
104	113-12	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pulchrum</i> (Kudr.) A. Filat.	Walidi	Wadi Ahan	Sohar	Batinah
105	113-5	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>hostianum</i> (Clem.)Mansf.	Missani	Wadi Ahan	Sohar	Batinah
106	113-6	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>hostianum</i> (Clem.)Mansf.	Hamira	Wadi Ahan	Sohar	Batinah
107	113-7	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>hostianum</i> (Clem.)Mansf.	Hamira	Wadi Ahan	Sohar	Batinah
108	115-1	<i>T. compactum</i>		<i>rigidcompactum</i>	<i>rigidcompactum</i>	<i>sedabense</i> A. Filat. et K.Hammer	Cooley	Buairdha	Ibri	Dhahira
109	115-2	<i>T. aestivum</i>	<i>aestivum</i>			<i>lutescens</i> (Alef.) Mansf.	Cooley	Buairdha	Ibri	Dhahira
110	115-4	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Cooley	Buairdha	Ibri	Dhahira
111	115-5	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Cooley	Buairdha	Ibri	Dhahira
112	115-6	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Cooley	Buairdha	Ibri	Dhahira

113	115-7	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudohostianum</i> (Flaksb.) Mansf.	Hamira	Buairredha	Ibri	Dhahira
114	120-11	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoerythrospermum</i> (Kudr.) A.Filat.	Shuaira	Al Raky	Wadi Bani Khalid	Sharquia
115	120-12	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Walidi	Al Raky	Wadi Bani Khalid	Sharquia
116	120-13-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Walidi	Al Raky	Wadi Bani Khalid	Sharquia
117	120-13-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> (compactoid)	Walidi	Al Raky	Wadi Bani Khalid	Sharquia
118	120-6-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>hostianum</i> (Clem.)Mansf.	Walidi	Al Raky	Wadi Bani Khalid	Sharquia
119	120-7-1	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>sedabense</i> K. Hammer et A. Filat.	Walidi	Al Raky	Wadi Bani Khalid	Sharquia
120	120-7-2	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticilinaza</i> Kudr.	Walidi	Al Raky	Wadi Bani Khalid	Sharquia
121	120-(120-5-1)	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Walidi	Al Raky	Wadi Bani Khalid	Sharquia
122	120-4(120-5-2)	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pulchrum</i> (Kudr.) A. Filat.	Walidi	Al Raky	Wadi Bani Khalid	Sharquia
123	120-3	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>hostianum</i> (Clem.)Mansf.	Walidi	Al Raky	Wadi Bani Khalid	Sharquia
124-1	120-(120-4-1)	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Walidi	Al Raky	Wadi Bani Khalid	Sharquia
124	120-2-3	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>sedabense</i> K. Hammer et A. Filat.	Walidi	Al Raky	Wadi Bani Khalid	Sharquia
125	121-(120-4-2)	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>sedabense</i> (Filat. et Hm.) A. Filat.	Sareeaa	Sedab	Taeen	Sharquia
126	121-2(121-1)	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>baladseetense</i> (Filat. et Hm.) A. Filat.	Walidi	Sedab	Taeen	Sharquia
127	121-3	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>baladseetense</i> (Hm. et Filat.) A. Filat.	Walidi	Sedab	Taeen	Sharquia
128	121-4	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>baladseetense</i> (Hm. et Filat.) A. Filat.	Walidi	Sedab	Taeen	Sharquia
128-1	121-4,5	<i>T. aestivum</i>	<i>aestivum</i>			<i>aestivum</i>	Walidi	Sedab	Taeen	Sharquia
129	121-5	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>baladseetense</i> (Hm. et Filat.) A. Filat.	Walidi	Sedab	Taeen	Sharquia
130	122-1	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>baladseetense</i> (Hm. et Filat.) A. Filat.	Walidi	Sedab	Taeen	Sharquia
131	126-1	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticilinaza</i> Kudr.	Cooley	Salma	Dhank	Dhahira
132	126-2	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticilinaza</i> Kudr.	Cooley	Salma	Dhank	Dhahira
133	126-3	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Sareeaa	Salma	Dhank	Dhahira
134	126-6	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Walidi	Salma	Dhank	Dhahira
135	127-1-1	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticilinaza</i> Kudr.	Cooley	Falaj Sudairen	Yanqul	Dhahira
136	127-1-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoleucospermum</i> (Kob.) Mansf.	Cooley	Falaj Sudairen	Yanqul	Dhahira
137	127-2-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoleucospermum</i> (Kob.) Mansf.	Cooley	Falaj Sudairen	Yanqul	Dhahira

138	127-2-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoleucospermum</i> (Kob.) Mansf.	Cooley	Falaj Sudairen	Yanqul	Dhahira
139	127-3	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoleucospermum</i> (Kob.) Mansf.	Cooley	Falaj Sudairen	Yanqul	Dhahira
141	127-6	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Cooley	Falaj Sudairen	Yanqul	Dhahira
142	128-10-1	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticilinaza</i> Kudr.	Cooley	Bahla	Bahla	Dakhilia
143	128-10-2	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticilinaza</i> Kudr.	Cooley	Bahla	Bahla	Dakhilia
144	128-10-3	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Cooley	Bahla	Bahla	Dakhilia
145	128-11	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Cooley	Bahla	Bahla	Dakhilia
146	128-1-2	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticilinaza</i> Kudr.	Cooley	Bahla	Bahla	Dakhilia
147	128-2	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticilinaza</i> Kudr.	Cooley	Bahla	Bahla	Dakhilia
147-1	128-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Cooley	Bahla	Bahla	Dakhilia
148	128-2-2	<i>T. aestivum</i>	<i>aestivum</i>			<i>aestivum</i>	Shalut	Bahla	Bahla	Dakhilia
149	100-1	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>omanense</i> A. Filat. et K. Hammer	Cooley	Iraqi	Ibri	Dhahira
150	100-1-1	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>omanense</i> A. Filat. et K. Hammer	Cooley	Iraqi	Ibri	Dhahira
151	100-1-2	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> (4), <i>pseudohostianum</i> (2)	Cooley	Iraqi	Ibri	Dhahira
152	100-1-3	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>meridionale</i> (Koern.) Mansf.	Cooley	Iraqi	Ibri	Dhahira
153	100-1-6	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Cooley	Iraqi	Ibri	Dhahira
155	100-3	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Cooley	Iraqi	Ibri	Dhahira
158	100-7	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Hamira	Iraqi	Ibri	Dhahira
158	100-7	<i>T. compactum</i>		<i>compactum</i>		<i>baladseetense</i> (Hm. et Filat.) A. Filat.	Hamira	Iraqi	Ibri	Dhahira
160	100-9	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>omanense</i> A. Filat. et K. Hammer	Cooley	Iraqi	Ibri	Dhahira
161	100-6-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Cooley	Iraqi	Ibri	Dhahira
162	100-6-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Cooley	Iraqi	Ibri	Dhahira
163	101-1	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Hamira	Khader Makattim	Khabura	Batinah
164	101-2	<i>T. compactum</i>		<i>compactum</i>		<i>baladseetense</i> K. Hammer et A. Filat.	Hamira	Khader Makattim	Khabura	Batinah
165	101-3	<i>T. compactum</i>		<i>compactum</i>		<i>baladseetense</i> K. Hammer et A. Filat.	Hamira	Khader Makattim	Khabura	Batinah
166	101-4	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Hamira	Khader Makattim	Khabura	Batinah
167	101-5	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Hamira	Khader Makattim	Khabura	Batinah
168	128-3	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Cooley	Bahla	Bahla	Dakhilia
169	128-4	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudovelutinum</i> (Kob.) Mansf., <i>hostianum</i> (Clem.) Mansf., <i>pseudoerythrospermum</i>	Cooley	Bahla	Bahla	Dakhilia
170	128-5	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>		Cooley	Bahla	Bahla	Dakhilia

171	128-6	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Shawie	Bahla	Bahla	Dakhilia
172	128-7	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Cooley	Bahla	Bahla	Dakhilia
173	128-8	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Cooley	Bahla	Bahla	Dakhilia
174	131-2-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Cooley	Qemat Barut	Qemat Barut	Qemat Barut
174-1	131-2-1	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticilinaza</i> Kudr.	Cooley	Qemat Barut	Qemat Barut	Qemat Barut
175	131-2-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Cooley	Qemat Barut	Bahla	Dakhilia
176	131-3	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pulchrum</i> (Kudr.) A. Filat.	Shuaira	Qemat Barut	Bahla	Dakhilia
177	131-4	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoleucospermum</i>	Cooley	Qemat Barut	Bahla	Dakhilia
178	131-5-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Shuaira	Qemat Barut	Bahla	Dakhilia
179	131-5-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Shuaira	Qemat Barut	Bahla	Dakhilia
180	131-6	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pulchrum</i>	Cooley	Qemat Barut	Bahla	Dakhilia
181	135-1	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>baladseetense</i> (Hm. et Filat.) A. Filat.	Walidi	Maqta	Taeen	Sharquia
182	135-2	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>baladseetense</i> (Hm. et Filat.) A. Filat.	Walidi	Maqta	Taeen	Sharquia
183	135-3	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>baladseetense</i> (Hm. et Filat.) A. Filat.	Walidi	Maqta	Taeen	Sharquia
184	135-4	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>baladseetense</i> (Hm. et Filat.) A. Filat.	Walidi	Maqta	Taeen	Sharquia
185	135-5	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>baladseetense</i> (Hm. et Filat.) A. Filat.	Walidi	Maqta	Taeen	Sharquia
186	136-1	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>baladseetense</i> (Hm. et Filat.) A. Filat.	Walidi	Maqta	Taeen	Sharquia
187	136-2	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>baladseetense</i> (Hm. et Filat.) A. Filat.	Walidi	Maqta	Taeen	Sharquia
188	137-1	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>maqtaense</i> (Filat., et Hm.) A. Filat.	Walidi	Maqta	Taeen	Sharquia
189	137-2-1	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>maqtaense</i> (Filat. et Hm.) A. Filat.	Walidi	Maqta	Taeen	Sharquia
190	137-2-2	<i>T. compactum</i>		<i>compactum</i>	<i>compactum</i>	<i>maqtaense</i> (Filat. et Hm.) A. Filat.	Walidi	Maqta	Taeen	Sharquia
191	138-3	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>hostianum</i> (Clem.) Mansf.	Khati	Al Raky	Wadi Bani Khalid	Sharquia
192	140-10	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pulchrum</i> (Kudr.) A. Filat.	Shuaira	Falaj Sudairen	Yanqul	Dhahira
193	140-11	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pulchrum</i> (Kudr.) A. Filat.	Cooley	Falaj Sudairen	Yanqul	Dhahira
194	140-1-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Cooley	Falaj Sudairen	Yanqul	Dhahira
194c	140-1-1	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticilinaza</i> Kudr.	Cooley	Falaj Sudairen	Yanqul	Dhahira
195	140-1-2	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>sedabense</i> A. Filat. et K. Hammer	Cooley	Falaj Sudairen	Yanqul	Dhahira
196	140-12-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudopyrothrix, pseudovelutinum</i>	Shuaira	Falaj Sudairen	Yanqul	Dhahira
197	140-14	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>hostianum</i> (Clem.) Mansf.	Shuaira	Falaj Sudairen	Yanqul	Dhahira
198	140-15-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Grade	Falaj Sudairen	Yanqul	Dhahira
199	140-15-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Grade	Falaj Sudairen	Yanqul	Dhahira

200	140-6(140-13)	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>densimenelikii</i> (Vav.)A.Filat.	Cooley	Falaj Sudairen	Yanqul	Dhahira
201	140-17	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>hostianum</i> (Clem.) Mansf.	Shalut	Falaj Sudairen	Yanqul	Dhahira
202	140-19	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoerythrospermum</i> (Kudr.) A.Filat.	Shalut	Falaj Sudairen	Yanqul	Dhahira
203	140-2	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>omanense</i> A. Filat. et K. Hammer	Cooley	Falaj Sudairen	Yanqul	Dhahira
204	140-21	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>hostianum</i> (Clem.) Mansf.	Cooley	Falaj Sudairen	Yanqul	Dhahira
205	140-22-1	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Shuaira	Falaj Sudairen	Yanqul	Dhahira
207	140-23	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudovelutinum</i> (Kob.)Mansf.	Grade	Falaj Sudairen	Yanqul	Dhahira
208	140-24	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pulchrum</i> (Kudr.) A. Filat.	Grade	Falaj Sudairen	Yanqul	Dhahira
209	140-26-1	<i>T. aestivum</i>	<i>aestivum</i>			<i>aestivum</i>	Hamira	Falaj Sudairen	Yanqul	Dhahira
210	140-26-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoerythrospermum</i> (Kudr.) A.Filat.	Hamira	Falaj Sudairen	Yanqul	Dhahira
212	140-4-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoleucospermum</i> (Kob.) Mansf.	Cooley	Falaj Sudairen	Yanqul	Dhahira
213	140-4-2	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>sedabense</i> A. Filat. et K. Hammer	Cooley	Falaj Sudairen	Yanqul	Dhahira
214	140-5	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koem.) Mansf.	Cooley	Falaj Sudairen	Yanqul	Dhahira
215	140-7	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koem.) Mansf.	Cooley	Falaj Sudairen	Yanqul	Dhahira
216	140-8	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koem.) Mansf.	Cooley	Falaj Sudairen	Yanqul	Dhahira
217	140-9-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koem.) Mansf.	Cooley	Falaj Sudairen	Yanqul	Dhahira
218	140-9-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Cooley	Falaj Sudairen	Yanqul	Dhahira
219	150-3	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>insigne</i> (Kudr.) A. Filat.	Cooley	Wadi Ahan	Ibri	Dhahira
220	150-5	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Cooley	Wadi Ahan	Ibri	Dhahira
221	150-6	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticilnaza</i> Kudr.	Cooley	Wadi Ahan	Ibri	Dhahira
222	143	<i>T. compactum</i>		<i>compactum</i>		<i>baladseetense</i> K. Hammer et A. Filat.	Walidi	Hadas	Taen	Sharquia
223	102-1	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Hamira	Khader Makattim	Khabura	Batinah
224	102-2	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Hamira	Khader Makattim	Khabura	Batinah
225	102-3	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Hamira	Khader Makattim	Khabura	Batinah
226	103-1	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Hamira	Al Khad	Khabura	Batinah
227	103-2	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Hamira	Al Khad	Khabura	Batinah
228	103-3	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Hamira	Al Khad	Khabura	Batinah
229	103-4	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Hamira	Al Khad	Khabura	Batinah
230	180-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudohostianum</i> (Flaksb.) Mansf.	Missani	Al Gum	Sur	Sharquia
231	180-3	<i>T. aethiopicum</i>	<i>vavilovianum</i>	<i>vavilovianum</i>		<i>tchertchericum</i> (Vav.)A.Filat.	Missani	Al Gum	Sur	Sharquia
232	116-1	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticilnaza</i> Kudr.	Cooley	Ibri	Ibri	Dhahira

233	116-2	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticulinaza</i> Kudr.	Cooley	Ibri	Ibri	Dhahira
234	116-3	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticulinaza</i> Kudr.	Cooley	Ibri	Ibri	Dhahira
235	116-4	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoerythrospermum</i> (Kudr.) A.Filat.	Sareeaa	Ibri	Ibri	Dhahira
236	117-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoleucospermum</i> (Kob.) Mansf.	Walidi big size	Al Drize	Ibri	Dhahira
237	117-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoleucospermum</i> (Kob.) Mansf.	Walidi big size with awns	Al Drize	Ibri	Dhahira
238	118-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoleucospermum</i> (Kob.) Mansf.	Cooley	Al Drize	Ibri	Dhahira
239	118-2	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Sareeaa	Al Drize	Ibri	Dhahira
240	119-2	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>sedabense</i> A.Filat. et K. Hammer	Cooley	Yanqul	Yanqul	Dhahira
241	119-3-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudoleucospermum</i> (Kob.) Mansf.	Cooley	Yanqul	Yanqul	Dhahira
242	119-3-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Cooley	Yanqul	Yanqul	Dhahira
243	119-3-3	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Shuaira	Yanqul	Yanqul	Dhahira
244	119-3-4	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Shuaira	Yanqul	Yanqul	Batinah
245	123-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Greda	Al Hajjar	Wadi Bani Kharus	Batinah
246	123-2	<i>T. compactum</i>		<i>rigidicompactum</i>	<i>rigidicompactum</i>	<i>muticulinaza</i> Kudr.	Shuaira	Al Hajjar	Wadi Bani Kharus	Batinah
247	123-3-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pseudovelutinum</i> (Kob.)Mansf.	Hamira	Al Hajjar	Wadi Bani Kharus	Batinah
248	123-3-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> , <i>ibraense</i>	Shuaira	Al Hajjar	Wadi Bani Kharus	Batinah
249	123-4	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>graecum</i> (Koern.) Mansf.	Sareeaa	Al Hajjar	Wadi Bani Kharus	Batinah
250	123-5-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>hostianum</i> (Clem.) Mansf.	Cooley	Al Hajjar	Wadi Bani Kharus	Batinah
251	123-5-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>hostianum</i> (Clem.) Mansf.	Greda	Al Hajjar	Wadi Bani Kharus	Batinah
252	124-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>hostianum</i> , <i>pseudoerythrospermum</i>	Walidi	Dhank	Dhank	Dhahira
253	124-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>hostianum</i> (Clem.) Mansf.	Mufsikha	Dhank	Dhank	Dhahira
254	124-3	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>pulchrum</i> (Kudr.) A. Filat.	Shuaira	Dhank	Dhank	Dhahira
255	124-4-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Cooley	Dhank	Dhank	Dhahira
256	124-4-2	<i>T. aestivum</i>	<i>aestivum</i>			<i>soharicum</i> K. Hammer et A.Filat.	Cooley	Dhank	Dhank	Dhahira
257	124-5-1	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>ibraense</i> K.Hammer et A.Filat.	Cooley	Dhank	Dhank	Dhahira
258	124-5-2	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>leucospermum</i> (Koern.) Mansf.	Cooley	Dhank	Dhank	Dhahira
259		<i>T. compactum</i>		<i>compactum</i>		<i>maqtaense</i> (Filat. et Hm.) A. Filat.	?			
260	J.Gebauer	<i>T. aestivum</i>	<i>hadropyrum</i>	<i>semirigidum</i>	<i>semirigidum</i>	<i>graecum</i> (Koern.) Mansf.		Jabal Al Akhbar		

REGULAR ARTICLE

Turkish wheat landraces: Population structure and function

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Abstract

The cultivated tetraploid wheat (*Triticum turgidum* ssp. *dicoccum*) was derived from wild wheat in southeast Anatolia at Karacadağ Mountain. There is a small core area in the region, where tetraploid wheat and many edible crop plants are cultivated. Settled human civilisation presumably started with wheat cultivation, after which traditional farmers developed landraces from germplasm collected after wheat domestication. Wheat landraces are adapted to different local environmental conditions; therefore, their gene pools display substantial genetic variation and have great potential as source of traits for good quality, resistance to adverse effects of biotic and abiotic stress factors, high yield and can be used to develop modern durum or bread wheat cultivars. Recently, however, high yielding modern wheat varieties are replacing landraces and cultivation areas and production of landraces decreased dramatically. This might lead to the loss or even extinction of landraces with invaluable germplasm. Therefore, *in situ* and *ex situ* conservation strategies should be supported to conserve the germplasm of landraces for future food security. Traditional farmers should be supported and encouraged to carry out on-farm conservation of landraces, where natural selection and continued evolution can generate new and more adapted germplasm.

Key words: Turkish wheat landraces, Genetic diversity, Turkish seed gene bank

Introduction

Domestication of wheat some 10,000 years ago increased the yield compared with other edible plants and cultural evolution might have been started with the settlement of communities (Feldman, 1995). Molecular genetics and archaeological data addressing that the Fertile Crescent is the place, where the cultivation of emmer wheat from the wild emmer wheat took place around 8th millennium BCE (Matsuoka, 2011; Salamini et al., 2002: cited in Oliveira et al., 2012). According to archeological data, free threshing tetraploid wheats (durum and rivet) existed in Near East and it has been supposed to be derived from domesticated emmer wheat (Salamini et al., 2002; Zohary and Hopf, 2000). Zohary and Hopf (2000) reported that emmer wheat might have given rise to durum wheat according to RFLP data,

obtained in their studies. As a result of hybridization between the D genome donor *Aegilops tauschii* and a domesticated tetraploid, which is supposed to be emmer wheat, bread wheat (*T. aestivum* L.) has been evolved (Lou et al., 2007: cited in Oliveira et al., 2012). In the domestication period the landraces existed before modern cultivars (Jaradat, 2011). While traditional farmers were growing landraces, they made good use of consumption meanwhile they let to their cultivation possible. The variety selection is very important decision for manufacturing and consumption considerations (Brush and Meng, 1998). The decision of variety selection with different traits is made according to farmers' specific demands and limitations display that their interests can be summarised as categories of agro-ecological and technological use (Bellon, 1996). These factors make the landraces cultivation preferable within farming systems of modern varieties are also grown (Brush and Meng, 1998).

Turkey is a geographical place, where many species originated and possibly also many plants domesticated in the same geographical area (Davis, 1985; Kaya et al., 1997; Tan, 1998; Bardsley and Thomas, 2005). Helbaek (1970) reported that the seeds of cultivated einkorn, emmer, free threshing

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wheat, pea, vetch, and bitter vetch identified at Çatalhöyük on the Konya plain of Turkey dated back to approximately 5800–5600 BC. The wide range of variability showed by these crops indicated that full-scale agriculture was already constructed when the place was first settled (cited in Harlan, 1975).

Turkish wheat landraces

In Turkey, diploid (cultivated einkorn), tetraploid (cultivated emmer and durum wheats), and bread wheat landraces are still growing on remote marginal eco-geographic farming lands by traditional farmers. Einkorn is a name given to diploid species that all have *AA* genomes with 14 chromosomes ($2n = 2x = 14$) in the genus *Triticum* (Rodrigues-Quijono et al., 1997). Einkorn includes a domesticated, hulled subspecies *Triticum monococcum* L. ssp. *monococcum* (with tough rachis), a wild subspecies *Triticum monococcum* L. ssp. *boeoticum* Baiss (with hulled grains and brittle rachis) and *Triticum urartu* Thum. ex Gandilj. According to some authors, *Triticum boeoticum* is a subspecies of *Triticum monococcum* L. (Kerby and Kuspira, 1987; cited in Rodrigues-Quijono et al., 1997) and two domesticated, free threshing subspecies *Triticum monococcum* L. ssp. *sinskajae* Rilat et Kurk. and *Triticum monococcum* L. ssp. *clusii* (Filatenko and Kurkiev, 1975; Szabo et al., 1994; cf. Vallega, 1995). In addition, hybrids between these taxa are fully fertile, whereas those with *Triticum urartu* Tum (also diploid wheat) are sterile (Dhaliwal, 1977). The progenitor of the male *AA* genome of tetraploid wheat *Triticum turgidum* L. ssp. *dicoccoides* (Körn. x Asch and Graebn) Thell, with genome formula *BBAA* was considered as *Triticum monococcum* (Kimber and Sears, 1987; Kimber and Feldman, 1987). Cultivated emmer wheat [*Triticum turgidum* L. ssp. *dicoccon* (Schränk) Thell.] is an allotetraploid species with a chromosome set of $2n = 4x = 28$ and genome formula *BBAA*. It is a primitive and no-free-threshing type of wheat. However, some researches, which displayed chromosome pairing evidences (Chapman et al., 1976; Dvorak, 1976), repeated nucleotide sequence evidence (Dvorak et al., 1988), and similar morphological characters such as red grain colour (Gandilyan, 1972) indicated that *T. urartu* might be donor of male *AA* genome of *T. turgidum*, while *Aegilopes speltoides* might be the progenitor of female *BB* genome (Dvorak and Zhang, 1990; cf. Waines, 1995).

Domestication of emmer wheat took place in the Karacadağ Mountains, west of Diyarbakır in south eastern Turkey according to previous studies

(Ozkan et al., 2005; Luo et al., 2007). Emmer wheat cultivation was progressed largely during the sixth millennium BC in the plains of Mesopotamia and western Anatolia. It was noteworthy that emmer wheat was the most commonly used cereal crop for farming in the Near East. Today, only traditional farmers are growing it on a limited scale in Ethiopia, Iran, Italy, Transcaucasia, Turkey and the Balkans. In Turkey, it is grown mainly on the northern part of Turkey and a few places in the southeast Anatolia. A collection of tetraploid wheats analysed by using AFLP markers to determine the origin of emmer and durum wheat domestication in south east Turkey (Ozkan et al. 2002). The domestication geography of tetraploid wheats was investigated by Ozkan et al. (2005) using AFLP molecular markers. They analysed the same plant materials that Mori et al. (2003) analysed by using cpDNA fingerprinting. According to previous studies (Ozkan et al., 2002; Ozkan et al., 2005), the existence of two very different genetic taxa of *T. dicoccoides* was confirmed (Sachs, 1953; Harlan and Zohary, 1966; Rao and Smith, 1968; cited in Ozkan et al., 2005). The one on the western part is composed of Israel, Syria, Lebanon and Jordan, while the one on the central-eastern part composed of samples mainly from Turkey and rarely from Iran and Iraq. It is supposed to be that the latter race might be the progenitor of domesticated germplasm (Mori et al., 2003; Ozkan et al., 2002; Salamini et al., 2004; cited in Ozkan et al., 2005). Additionally, the population from Karacadağ displayed intermixed genomic structure with some Iran-Iraq lines also support that Karacadağ population was the putative progenitor of domesticated genotypes (Ozkan et al., 2005).

Nowadays, a tetraploid wheat species, durum wheat [*Triticum turgidum* ssp. *turgidum* convar. durum (Desf) MacKey] with genome formula ($2n = 4x = 28$; *AABB*) is growing in the area of Middle and Near East, where durum wheat was originated and diversified as many other plant species the Mediterranean Basin, North Africa, Australia, Argentina, India, and the United States of America. Durum wheat is one of the important cereals in human diet and used to make bulgur, couscous, pasta, in some places even for bread making and homemade macaroni.

Bread wheat is the major prominent cereal in the world due to its high nutritional value, adaptable to wide eco-geographical conditions, easy farming, and storing conditions. As a hexaploid wheat species, bread wheat [*Triticum aestivum* L.] has genome formula of *AABBDD* with

a chromosome set of $2n = 6x = 42$ and its landraces have been growing widely all over the Anatolia since ancient times. Nevertheless, because of increase in interest of high yielding modern varieties, bread wheat landraces are disappearing with their invaluable traits.

The genetic diversity in Turkish wheat landraces

Genetic diversity in nature became known mainly in population genetics by isozyme diversity studies in plants, animals and humans (Lewontin, 1974), and was only later followed by proteins (Bushuk and Zillman, 1978) and DNA diversity analysis (Nevo, 1988). Endosperm proteins and isozyme systems are frequently used in several phylogenetic analyses of wheat species.

Gliadins are a group of endosperm proteins and separated into α , β , γ , and ω gliadin subunits on electrophoresis at low pH (pH 3.1) (Bushuk and Zillman, 1978). Gliadin protein subunits are coded by six *Gli* loci, found on the short arms of homeologous group chromosomes of 1 and 6 (Payne et al., 1982). The *Gli-1* loci coding for ω , γ , and some β gliadins are placed on group 1A, 1B, and 1D chromosomes, while *Gli-2* loci coding for α , β , and γ gliadins are placed on group 6A, 6B, and 6D chromosomes (Metakovsky and Sozinov, 1987; Payne et al., 1988). Each *Gli* locus consists of 3 to 10 genes (Payne, 1987), and they behave like a single Mendelian trait and inherited together (Sozinov and Popereleya, 1980). The gliadin proteins expressed by those linked genes, called as gliadin blocks. The differences in number, mobility, and staining intensity of gliadin protein subunits are the products of allelic variants of gliadin blocks (Kudryavtsev et al., 1996). Some of the gliadin and glutenin subunits, as valuable biochemical markers, were found to be related with good bread making and pasta quality (Payne et al., 1980; Gupta and Shepherd, 1988; Pogna et al., 1990). The 2 gliadin protein subunits, γ -42 and γ -45 encoded chromosomes 1B correlated significantly with poor and good quality respectively. The glutenin subunits fractionated into two groups, which are low-molecular-weight (LMW) and the high-molecular-weight (HMW) subunits (Payne and Lawrence, 1983) according to their molecular weight on SDS-PAGE). The tightly linked genes, placed on the long arms of chromosomes 1A, 1B, and 1D encoded HMW-glutenin subunits, which are classified as larger x-type subunits and smaller y-type subunits (Payne et al., 1981).

The genetic diversity in Turkish cultivated einkorn wheat (*Triticum monococcum* L. ssp. *monococcum*) (Şan et al., 2013 unpublished data;

Peşkircioğlu et al., 1998) and diploid wheat species (*Ae. caudata*, *Ae. mutica*, *Ae. speltoides*, *Ae. umbellulata*, *T. monococcum* and *T. urartu*) (Peşkircioğlu et al., 1998) landraces were analysed. Also Karcicio (2003) assessed genetic diversity by using isozyme systems among *Triticum* ssp. (*Triticum monococcum* L.) and *Aegilops* spp. (*Aegilops mutica* Boiss., *Aegilops umbellulata* Zhuk., *Aegilops speltoides* Tausch, *Aegilops triuncialis* L., *Aegilops biuncialis* Vis., *Aegilops cylindrica* Host, *Aegilops columnaris* Zhuk., and *Aegilops ovata* L.).

The endosperm proteins and isoenzymes were used several times to determine genetic diversity in Turkish wheat landraces. The genetic diversity was investigated for the first time in terms of gliadins (Özbek et al., 2011), high molecular weight (HMW)-glutenin subunits (Özbek et al., 2012) and isozyme systems (Özbek et al., 2013) in Turkish cultivated emmer wheat [*Triticum turgidum* L. ssp. *dicoccon* (Schrank)] landraces and polymorphism at molecular level with using RAPD markers was investigated by Yeşbek (2007).

Turkish durum wheat (Akçura, 2009; Sayaslan et al., 2012; Zencirci and Karagöz, 2005) and bread wheat (Akçura and Topal, 2006; Kara and Akman, 2007) landraces were assessed to determine the genetic diversity by several authors according to some quality related morphological traits. Ozkan et al. (1998) analysed HMW-glutenin subunit variation in durum wheat landraces of Turkey. Akar and Özgen (2007) investigated genetic diversity at molecular level using RAPD markers in durum wheat, whereas Sönmezoğlu et al. (2012) investigated genetic diversity at molecular level using SSR markers in bread wheat in Turkey.

Population structure

The population structure analyses are important to determine the local adaptations, if the differences in allele frequencies between populations are maintained due to natural selection and genetic differentiation within and between subpopulations of metapopulations.

The analysis of endosperm protein polymorphism in Turkish cultivated einkorn wheat (Şan et al., 2013 unpublished data) indicated substantial genetic diversity in terms of gliadin. According to genetic diversity analysis of endosperm proteins (Özbek et al., 2011; Özbek et al., 2012), isoenzymes (Özbek et al., 2013), and RAPD (Yeşbek, 2007) markers in Turkish cultivated emmer wheat landraces, great amount of genetic diversity was observed. Özbek et al. (2011) showed that emmer wheat landraces populations

had some gliadin proteins such as ω -45 and gliadin ω -35, which are correlated significantly with dough technological qualities (Turchetta et al., 1995). Some HMW-glutenin alleles were distributed locally (in only two populations), while other alleles were distributed sporadically (in more than three populations). The spatial heterogeneity has significant effect on genetic diversity and genetic differentiation of Turkish landraces populations. The change in geographical conditions such as change in latitude might have effects on differentiation in elevation, soil type, duration of radiation exposure time, and water availability and, results as genetic and morphological diversity in landraces (Özbek et al., 2012).

The studies investigating polymorphism in some morphological traits (percent vitreousness, pearling index, grain protein content, seed yield and thousands kernel weight, time frame for germination- tillering, germination- shooting, germination- heading, germination- maturity, tillering- shooting, tillering- heading), tillering- maturity and heading- maturity) were assessed by Zencirci and Karagöz (2005), whereas some morphological traits (plant height, spike length, grain number per spike, biological yield, and resistance to lodging etc.), pathological (stripe and leaf rusts), and technological traits (1000 kernel weight, hectolitre weight, protein ratio, SDS sedimentation etc.) were assessed by Akar and Özgen (2007). The morphological studies indicated a wide range of variability in Turkish durum wheat landraces.

The results of previous studies (Yeşbek, 2007; Peşkırcioğlu et al., 1998; Karcicio, 2003; Özbek et al., 2011; Özbek et al., 2012; Özbek et al., 2013; Şan et al., 2013 unpublished data) indicated that Turkish wheat landraces have doubtless great genetic diversity in terms of protein and isoenzyme polymorphism. The landraces populations have great genetic diversity within population than between population, while a great genetic differentiation is also observed between populations. There are several reasons for this great amount of genetic differentiation. Traditional farmers' seed exchanging system and environmental factors associated with this level of genetic differentiation in Turkish wheat landraces. Seed management by traditional farmers is influenced by many constraints, including agro-ecological, economic, and socio-cultural, as well as by who can grow the varieties using a common genetic background. In traditional agricultural systems, farmers generate and conserve new varieties, most of which are landraces. As these

farmers are also consumers of their own products, they decide which seeds to save or recycle and which to dispose of. This practice makes the genetic content of the landraces very dynamic. In contrast to the high gene flow estimates observed in other landraces, the low gene flow estimate observed in Turkish landraces (Özbek et al., 2011; Özbek et al., 2012; Özbek et al., 2013) may suggest that the seed exchanging system might not be sufficiently functional among the farmers because they produce a low yield of emmer wheat, only enough to supply, their own personal needs. Therefore, they may recycle the same material without replacing or mixing it with other farmers' varieties, resulting in the great genetic differentiation observed among the populations. Although farmers have selected some genotypes based on their agronomical characters by causing genetic drift, environmental factors such as the climate, which changes from year to year, can accelerate the effects of natural selection. As a result, genotypes that are able to survive contribute to the genetic diversity of the germplasm of landrace populations. Therefore, traditional farmers should be encouraged to run seed exchange systems as the maximum functionality so as to avoid unity. Statistical tests (Pearsons' correlation, multiple regression, and Principal Component Analyses) indicated that climatic and geographic variables in combination with each other affected genetic diversity of endosperm protein and isoenzymes at a considerable level in Turkish cultivated emmer wheat landraces (Özbek et al., 2011; Özbek et al., 2012; Özbek et al., 2013). The selection pressure applied by traditional farmers on the traits according to their own criteria and the seed exchange facilities between farmers have given rise the good bread making quality traits associated with high genetic variability in emmer wheat landraces.

Turkish landraces as genetic resources

A landrace may display variation for many traits, which are evolved because of natural selection and by traditional farmers to a limited extent in the environment, where it is inhabited, due to its admixed genotypes. Therefore, the landraces, which are bearing desirable traits such as cold, heat and drought tolerance; time to heading/maturity and seed filling duration; resistance to diseases caused by plant pathogens and other adverse environmental stress factors (Jaradat, 2011).

Since, the landraces are the products of traditional farming system resulted from many years and traditional farmers impute the value on

landraces according to economic analysis of variety choice and ethno botanical information about uses of and towards different varieties (Braush, 1991). Therefore, the studies on screening the germplasm of landraces, which is recognised as major genetic resources, are vitally important. Particularly the studies about economic analysis, ethno botany, and genetic structure of landraces play important role for future aspects. In Turkish wheat landraces, the genetic variation according to biochemical characters, endosperm proteins and isoenzymes, (Ozkan et al., 1998; Peşkircioğlu, 1998; Karcicio, 2003; Özbek et al., 2011; Özbek et al., 2012; Özbek et al., 2013), variation according to different environments (Zencirci and Karagöz, 2005), genetic variability and interrelationship among grain yield and some quality traits (Akçura, 2009; Sayaslan et al., 2012), genetic diversity as revealed by molecular markers (Yeşbek, 2007; Sönmezoğlu et al., 2012) to determine new durum wheat germplasm resistant to biotic and abiotic stress factors (Akar et al., 2009) displayed that Turkish wheat landraces might have a great potential to have some traits such as higher yield, good bread making, or pasta quality, resistance to rusts, and some other desirable quality traits in their large gene pool reservoir, which was used to developed durum and bread wheat varieties. Although Turkish wheat landraces have all these great potential, nevertheless, they were not used intensively in breeding programs. In Turkey, cultivated bread wheat and durum varieties such as Sivas 111-33, Sertak 52, Ak 702 (Bread wheat) and Kunduru 1149 (Durum wheat) were developed in breeding programs and distributed. In these programs, Turkish wheat landraces have been used as parental Turkish wheat varieties (Karagöz and Zencirci, 2004). The Turkish wheat landraces should be managed practically usable in more breeding programs as genetic resources.

In breeding, stem solidness is a consequential trait for resistance to wheat stem sawfly- a serious pest insect in West Asia and North Africa. Damania et al. (1997) reported that Turkish durum landraces gene pool contained considerable amount of germplasm to be used in selective breeding programs for this trait.

Some γ -gliadin and/or low molecular (LMW)-glutenin proteins found to be correlated strongly with each other and they related with viscoelastic properties of gluten that affected cooking quality of pasta products. γ -gliadin-45 and LMW-2 glutenin subunits displayed correlations with adequate gluten strength and good pasta quality, while γ -

gliadin-42 and LMW-1 glutenin subunits displayed correlations with weak gluten strength and low cooking quality (Damidaux et al., 1978; Joppa et al., 1983; Autran et al., 1986; Pogna et al., 1990; Fares et al., 1997). Yıldırım et al. (2011) represented that the landraces, analysed in their studies carried out carrying γ -gliadin 45 and LMW-2 glutenin proteins correlated with proper gluten strength and superior pasta-cooking quality.

Emmer wheat has some useful traits, which can be used for durum and bread wheat breeding such as resistance to leaf diseases and common bunt (Corazza et al., 1986), resistance to yellow rust (Damania and Srivastava, 1990), immune to powdery mildew, (Jakubziner, 1969), displaying resistivity against to fusarium head blight or scab (Oliver et al., 2008). It is also known that, *Ep-1* locus is an important marker for an agronomic trait, the linkage between the genes encoding *Ep-1* located on homeoallelic series of *Triticeae* group 7 chromosomes and a gene conferring resistance to eyespot disease was demonstrated first time by McMillin et al. (1986) (cited in Koebner et al., 1987). When the amount of genetic diversity observed in emmer wheat was taken account, Turkish emmer wheat landraces are representing a great gene pool reservoir to be surveyed and promising for future breeding programs.

Socioeconomic aspects and uses of Turkish wheat landraces

The agriculture of emmer and einkorn cultivation in Turkey exhibits both agronomic practices and socioeconomic aspects (Karagöz, 1995). The cultivation and yields of hulled wheats decreased from 1948 to 1993. The area sown (ha) decreased from 107.758 to 12900, while the yield decreased from 825 to 1,240 (kg/ha). Another important finding is that 72% of working-aged Turkish males from rural areas migrate seasonally to larger provinces as unskilled workers in order to earn a yearly income to support their families. In terms of land use, forests dominated with an average of 55%, and the remainder of the area was cultivated. Hulled wheat grown in sloping, marginal forest areas is not suitable for field crop cultivation. Crop resources are scarce and far from adequate in satisfying the needs of the population (Karagöz, 1995).

Hulled wheat is cultivated in marginal areas and in organic farming conditions, where modern varieties are not able to develop their production potential very well because they were selected for different land and climatic conditions. Einkorn and emmer wheat are grown at the North Transitional

Zone of Turkey by poor peasants, who are unable to grow other crops in that area. They use most of the emmer wheat as fodder for animals; with the remaining seeds, they make local foods such as bulgur, homemade macaroni (erişte) and a soup that is mixed with other ingredients, including wheat. Recently, there has been renewed interest in healthy foods, and in particular, for the products generated by organic farming. This increased interest can be used to further the advantages of using landraces.

Vallega (1979) reported that when the cereal crops such as einkorn, barley, and durum wheat are grown under unfavourable conditions, the production rate of einkorns for the amount of protein yield equal to or higher than the others did. Stallknecht et al. (1996) reported that the amount of protein, ranged between 50% and 75% found in einkorn grains was higher than the grain of hard red wheats displayed (12.5% to 73.5%).

Hulled wheat cannot compete with high-yielding varieties economically, but it can compete in the areas of flavour and healthy food quality. Turkey does not have a commercial market for emmer wheat. However, in Italy, there is a small-scale commercial market for emmer wheat, also known locally as “farro”. Although the Italian market for emmer wheat has not yet matured and stabilised (D’Antuono and Bravi, 1995), a similar yet modified commercial model could be developed in Turkey. Commercialised products of processed emmer wheat may provide an alternative method for contributing to the economy; this would specifically benefit the poorer communities, who grow emmer wheat. Commercial manufacturers and industries, as well as the public should focus on creating a market for such products (D’Antuono and Bravi, 1995).

Conservation strategies

Recently, increase in agricultural production is the result of growing a few high-performing varieties, and formal regulations taken for limiting the trade of local varieties to the advantage of high-performing varieties in some countries (Holden et al., 1993), while genetic diversity decreased dramatically in cultivated forms of crops. Therefore, investigation of genetic diversity in populations is important step to use germplasm collections for planning breeding programs and to decide for conservation strategies (Tadesse et al., 2001). The significance of assessment of genetic variation in landraces has been highlighted by Convention on Biological Diversity, signed by 172 countries at Rio de Janeiro in 1992 (Mugnozza, 1995). One of the best strategies for conservation of

genetic variation in local varieties and landraces of cultivated modern varieties is “on farm” conservation (Pagnotta et al., 2004). For conservation strategies, genetic resources should be conserved by using both *ex situ* and *in situ* conservation methods. The seeds of most plant species can be stored under appropriate conditions up to 10-50 years. For conservation strategies of genetic resources, *ex situ* is a very hard and obligated process. Because, the seeds should be stored at -20°C temperature in cold rooms. At this temperature seeds might be kept 10-50 years. For long-term conservation, the seeds should be controlled for viability test every 5-10 years and cultivated in the fields to get fresh seeds to increase the sustainability of those genetic resources. For this, large farming areas for cultivation, human power for harvesting and other breeding activities, and funds for covering all these considerably expensive expenses are needed. In addition, during these breeding activities there are some risks for selfing plants, which may cross-pollinate, or mixing the seeds of different genetic materials by mistaken.

In Turkey, genetic resources are conserved mainly according to *ex situ* conservation method. A great attention should be taken to prevent reduction in genetic diversity due to strong selection factors and interspecific completion during *ex situ* regeneration of seeds (Figliuolo and Perrino, 2004). The genetic drift is a great risk for losing genetic diversity over time in small size finite populations according to genetic theory (Hartl and Clark, 1997). Also in *ex situ* conservation, limited number of samples is conserved; as a result all the diversity in landraces germplasm could not be collected in the gene bank. Therefore, for conservation of genetic diversity in landraces, farmers in traditional farming systems should be encouraged to continue traditional farming practices through the financial support of state agricultural regulation laws similar to the support given to modern agricultural farming. This step is essential since landraces are important genetic resources for demands of future crop improvement and world food security. However, in Turkey, the trade of local seeds is forbidden by a State Seed Law (5553). Farmers can only use the seeds, which are certified by Food, Agriculture, and Livestock Ministry. Traditional farmers found a creative way recently. In some provinces, the traditional farmers hold a seed exchange festival. They exchange any kind of plant seeds in the festival. These festivals are supported and organised by some civil organisations like Ecological Producers Association, and municipalities of those provinces. The traditional

farmers claimed their organic seeds and they are aware of the importance of those local seeds for ecology, genetic diversity, and future food security of the world. During these festivals, they hold meetings, panels, play dramas, and musicals to inform the people about the importance of traditional farming of local seed varieties. With the contribution of these seed exchange festival, landraces will get more dynamic and diversified genetic structure.

Turkish Seed Gene Bank (SGB)

Turkish Seed Gene Bank (SGB), which has a capacity of 250 000 specimens was founded in 2010 and took its place among the worldwide gene banks. SGB has 1,043 m³ cold space volumes and contains following sections; documentation, seed preparation including drying and packaging units, breeding and characterisation, seven cold rooms, a seed physiology laboratory, a molecular biology laboratory, a herbarium, which has a capacity of 60 000 specimens, and a screening room. Currently, approximately 34 000 specimens are stored in cold rooms of SGB, 3000 of which are wheat landraces, while in the herbarium 6000 specimens are stored as *ex situ* conservation. The collection and usage of wild wheat, and wheat landraces are regulated by state laws and under control of the Ministry of Food, Agriculture, and Livestock (MFAL) of Turkey. Researchers have to get permission from MFAL to collect wild wheat, and wheat landraces and to acknowledge, how they benefit from the germplasm of wild wheat, and wheat landraces as genetic resources. In addition, those researchers have to send some of the specimens, which they collect to MFAL gene bank. In this way, genetic resources of wild wheat and all wheat landraces will be protected and kept under control of single hand. The research institutions belong to MFAL and universities carry out some studies about screening the genetic structure and diversity of wild wheat, and wheat landraces germplasm, and their usage for the benefit of breeding programs. In addition, they plan conservation strategies for what and how to conserve for future perspective.

Conclusion

Although, the previous studies indicated that Turkish wheat landraces populations had high level of variability within and among populations, the cultivation area of hulled wheats or landraces is dramatically reduced nowadays. The replacing high yielding modern wheat varieties with hulled wheats or landraces might be caused to risk of extinction of invaluable landraces germplasm as genetic

resources. Therefore, for future crop improvement, genetic resources of landraces should be considered to be conserved urgently. For planning conservation strategies, beside *ex situ* conservation, *in situ* conservation should be considered more seriously and planned consciously to maintain dynamic and high genetic diversity level in their natural evolutionary history. Because, landraces are the guarantee of future food security of the world, therefore conservation strategies should be undertaken not only as a national process but also should be undertaken as a global process.

For future requirements, we need to make decisions what and how to conserve appropriately. Therefore, agronomical features of genetic structure, protein amount and quality, and genetic upload of landraces should be taken account. In this context, the genetic structure and evolutionary history of Turkish wheat landrace populations should be assessed in detailed analysis to plan appropriate conservation strategies. For breeding programs, Turkish wheat landraces, which have genetically diversified genotypes for peculiar traits such as high protein content could be utilised as it was done in previous studies.

We should claim our local seed varieties, if we would like to leave a secured and fruitful life for our next generations.

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REGULAR ARTICLE

Wheat Landraces of Turkey

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Abstract

Turkey falls within Vavilov's Center of origin and harbors large genetic diversity of several economically important crop species. Wild crop relative, such as wild einkorn, wild emmer, wild barley, wild oats, wild rye and their respective domesticated forms, in addition to a multitude of other crop species, have been cultivated for millennia in several parts of Turkey, but especially in the northern part of the Fertile Crescent. Turkish farmers developed landraces from these crops; however, these landraces and the indigenous knowledge gained over many generations are being lost due to several anthropogenic and other factors. Landraces of wheat and other major and minor crops still play an important role in the livelihood of small scale farmers in Turkey. This paper reviews and contrasts the current status of Turkey's main wheat landraces with their past; and suggests specific strategies for their maintenance.

Key words: Wheat landraces, Turkey, genetic diversity

Introduction

There are various definitions for "landrace" or "variety". Harlan (1995) describes the landraces as "balanced populations – variable in equilibrium with both environment and pathogens and genetically dynamic". They are defined as "local" when seed from that variety has been planted in the region for at least one farmer generation (Louette, 2000). In an attempt to provide a clear definition to "landrace", Zeven (1998) claims that due to its complex and indefinable nature, an all-embracing definition cannot be given. However, Zeven suggests the following: "*an autochthonous landrace is a variety with a high capacity to tolerate biotic and abiotic stress, resulting in a high yield stability and an intermediate yield level under a low input agricultural system*". For the definition of landrace, Bioersvity International agrees upon the following definition: "*A landrace of a seed-propagated crop is a variable population, which is identifiable and usually has a local name. It lacks 'formal' crop improvement, is characterized by a specific adaptation to the environmental conditions of the area of cultivation (tolerant to the biotic and*

abiotic stresses of that area) and is closely associated with the uses, knowledge, habits, dialects, and celebrations of the people who developed and continue to grow it" (Biodiversity International, 2013). Common points in the definitions are, landraces undergo an adaptation process for certain length of time and possess some degree of tolerance to stress conditions.

Background information

Agriculture and horticulture have long history in Turkey. The information gathered from several excavations suggest that agriculture started to evolve in Anatolia almost 10,000 years ago. Anatolia hosted several civilizations in the past and it was a path way between Asia and Europe during the history (Harlan, 1995; van Zeits and de Roller, 1995; Karagöz et al., 2010). Recent excavations in Göbekli Tepe of Şanlıurfa Province have a potential to shed light on the periods prior to known date of agriculture (Bird, 1999). Throughout history, the Turkish people benefited a lot from local varieties.

Farmers, for over 500 generations have given us a priceless heritage of diverse germplasm. They gradually improved their material by selecting for several desirable characteristics such as bigger fruits (grain), homogenous germination, non-shattering, non-lodging, homogenous ripening, better tasting and quality and so on. Changing environmental conditions also contributed a lot for the landraces to develop genotypes that are better adapted to conditions where they were grown.

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Harlan (1995) lists the following steps usually followed as wild species, that may have been initially gathered were gradually brought into cultivation; loss of natural dispersal mechanism, rapid germination, larger seeds, simultaneous ripening, loss of mechanical means of protection, color changes and loss of toxic or bitter properties. Final product through time was a good accumulation of morpho-physiological traits conferring adaptability to stress environments (Jaradat, 2013).

Wheat has been a staple crop in the Anatolian region since prehistoric times. Anatolia has been home to vast numbers of farming cultures, from the initial waves of Neolithic migrants to modern times. Early Indo-European cultures, Hittites, Hellenic and Byzantine cultures, Romans, and Turkic cultures have successively occupied Anatolia since the beginnings of agriculture there. As other crops in their cradle areas of crop domestication, the diversity of wheat in Anatolia is large, as farmers have identified, multiplied and preserved them for millennia (Brush, 1995). Farmers in northern Turkey still grow emmer (*Triticum dicoccon*) and einkorn (*Triticum monococcum*), two primitive species, and the first wheat types to come into cultivation (Karagöz, 1996; Nesbitt, 1995; Guiliani et al., 2009). It is reported that emmer is also grown at 6 villages in Caucasian part of Turkey through participatory sustainable projects run by a local NGO (Anatolia Foundation, 2013). Bread wheat (*Triticum aestivum*) dominates Anatolia, although the durum wheat (*Triticum durum*) is also common.

Varietal richness in cultivated and natural plants attracted several other scientists in the past. Vavilov, Zhukovsky and Harlan (Harlan, 1950) were among them. In the same period as Gökgöl, well known Russian scientist Zhukovsky conducted 3 collecting missions to Turkey during 1925-1927. Zhukovsky was encouraged by Vavilov and his missions were supported by The Botany Society of the Soviet Union. The author paid praise to M. Gökgöl for his generous assistance during the missions (Zhukovsky, 1951). During three years of hard work in Turkey, Zhukovsky collected around 10,000 samples of cereals, forages and vegetables. The material was an enormous contribution to plant varieties of the Soviet Union (Zhukovsky, 1951).

Among the crop species, Turkey's wheat variation has always received greater attention since the beginning of 20th century. At the first quarter of 20th century, pioneering Turkish scientist Mirza Gökgöl collected wheat landraces from all over Turkey and evaluated them for basic characteristics. Gökgöl identified about 18.000 types of wheat and among them he identified 256 new varieties. His publications are still the most notable sources for the breeders and scientists dealing with plant genetic resources. The analyses of these material convinced Gökgöl that almost all wheat varieties existing in the world were present in Turkey and that Turkish landraces provide an endless treasure to the breeders (Gökgöl, 1935; Gökgöl 1939; Gökgöl, 1955).

Turkish farmers cultivated their landraces widely until the second half of 20th century. After the World War II, a program was started in Turkey through an agreement with Rockefeller Foundation. Although it was a modest start in agriculture research, mechanization, use of fertilizers and chemicals, it resulted in unexpected consequences. Among several plant groups involved, wheat program had the greatest impact. It didn't take long for the new varieties to replace the landraces. The heritage begun to be demolished after so called high yielding "Mexican wheats" were introduced to the country. Initially some of those high yielding semi dwarf varieties yielded as much as four times the local varieties with suitable input. Although the country has also introduced some of previously unknown wheat diseases, it was assumed as "the green revolution" and enjoyed by Turkish farmers those days.

Table 1 gives a brief list of wheat yield values through time from late Ottoman Period (before the establishment of Republic of Turkey), before high yielding varieties (HYV's) and after introduction of HYV's up to 2012. Although the values suggest that there is a consistent yield increase after the introduction of high yielding varieties, it is also the period when farmers used agricultural inputs extensively. If the years with too little yield, due to wars and severe droughts are excluded, over 1 ton/ha during Ottoman Period can be regarded excellent in the absence of agricultural mechanization and use of inputs.

Table 1. Area sown to wheat, production and grain yield since late 19th century (Gökgöl, 1935; TÜİK, 2013).

Period	Year	Area sown (000 ha)	Production (000 t)	Yield (kg/ha)
Late Ottoman	1897	2.907	2.763	950
	1909	2.566	3.285	1.280
	1914	2.337	4.009	1.715
	1925	3.130	1.075	344
Before high yielding varieties	1935	3.430	2.521	735
	1945	3.742	2.189	585
	1955	7.060	6.900	977
	1965	7.900	8.500	1.076
	1975	9.250	14.750	1.594
After high yielding varieties	1985	9.250	17.000	1.818
	1995	9.400	18.000	1.910
	2005	9.250	20.010	2.163
	2012	7.530	20.100	2.670

Reasons for landrace cultivation

It is evident from the past experience that agricultural research generally addressed to the most promising areas by concentrating on species with economic importance. Doing so the researchers have saturated the most productive regions by providing suitable high yielding varieties and all the necessary technical information including agronomy packages developed for specific regions.

Traditional farmers in marginal areas have always been neglected by the researchers. In other words farmers of the marginal areas were left with all the elements of their traditional way of farming. Most of the innovations developed for the suitable environment, did not fit to the marginal areas. Therefore traditional farmers in marginal regions were more likely to maintain their landraces (Harlan, 1995).

Several factors including physical, climatic, socio-economic, market facilities, pricing policies, and so on, play role in cultivation of landraces. Multiple farmer concerns such as conformity for special food production, yield, risk and quality concerns contribute to the persistence of landraces. Household characteristics in forming variety choice will also affect the household's perceptions of the importance and value of landraces (Brush and Meng, 1998).

Reliable yield level is another reason for retention of landraces, because they are low risk option in the marginal conditions, resulting in fewer poor production years (Bardsley and Thomas, 2005). While the average annual production is likely to be lower with traditional varieties in marginal areas, they are perceived by farmers as producing more in the worst years than the modern varieties (Bardsley and Thomas, 2005). Genetic

diversity within and between local varieties plays a role in seed production, albeit a small amount, in disaster years. The landrace does not necessarily have a level of tolerance to diseases, but being heterogeneous they may be able to offer some level of protection against extreme agronomic conditions (Bardsley and Thomas, 2005).

Access to markets plays an especially important role in the decision to cultivate traditional varieties. Households with fewer market sales are characterized by the smallest amount of total land owned as well as a relatively small percentage of available irrigated land (Brush and Meng, 1998).

Consumption attributes of a variety are reported to be important to the farm household, on farm cultivation is the best solution to guarantee availability (Brush and Meng, 1998). Advantages of Kırık landrace in East Anatolia High quality and white grain for white unleavened lavash bread, High value marketable product locally, Short-growing season, Facultative wheat, Low risk of production, Good straw, no awns (Bardsley and Thomas, 2005)

Variety choice is based on multiple household objectives and can not be attributed only to yield. The interaction among the various attributes is likely to play an important role. Yield attributes are ranked higher for modern varieties while traditional varieties are ranked higher in terms of taste and baking quality. Traditional varieties are also associated with better drought resistance attributes (Brush and Meng, 1998).

Present status

As it was stated above, a variety is regarded as "local", if it has been planted at least for one farmer generation (Louette, 2000). Assuming that farmers of Turkey have been practising agriculture for

10.000 years, one can easily figure out that thousands of landraces must have been transferred from father to son for over 500 generations. Time elapsed is long enough for especially annual crops to develop genotypes adapted to biotic and abiotic stress conditions in relatively large geography.

It is quite evident that landraces covered all of the arable lands some 50 years ago. Dalrymple (1986) claims that about 50% of Turkey's wheat area was planted in HYV's in 1984, by the varieties selected among high quality farmer cultivars and introduced varieties. No official figure is available at the moment about the ratio of landraces in each plant groups. What we can do is try to make a rough estimation by means of indicators of landrace cultivation. For that, first thing to do is to assess the reasons for cultivating landraces. A number of factors can be listed here for the reasons why the farmers continue or quit cultivating landraces. Most of the reason are universal and a few of them may be peculiar to Turkey.

Land size is an important indicator for productivity of agricultural system. Population increase possesses great pressure in Turkey on land size. Current inheritance system anticipates sharing the inherited property equally among the successors. Consequently land is fragmented into tens of plots in a few generations. Average farm size is 6,1 ha and about 65 % of the enterprises have a farm size lower than 5 ha. We should underline the fact that above mentioned factors generally act in favor of landraces cultivation. Another peculiarity of agricultural production system is that about 51 % of the agricultural enterprises are fragmented into more than 6 plots (Güven, 2010; SIS, 1994; SIS, 2004).

Karagöz (1996) reports that hulled wheat landraces cultivation is still practiced in villages of Sinop Province (north) by subsistence farmers majority of whom have farm size smaller than 5 ha without irrigation facility. Average number of plots per house holds is 16, there is no market for the crop and the crop is mainly grown as animal feed. Although several high yielding wheat varieties were tested to replace hulled wheat species, none of them overcome the yield of hulled wheats. This was due to the fact that hulled wheat landraces are better adapted to adverse conditions than the improved varieties. Hulled wheat is considered an indicator of poverty.

In an another study performed in north-north western transition zone (Bolu, Kastamonu, Bilecik, Eskişehir and Kütahya Provinces) following points have been highlighted: over 50 % of the farmer peasants were more than 50 years old, all with

farming background of at least 20 years, fertilizer is only used for wheat, relation of the farmers with local extension service is weak, 47 % of the farms have no irrigation facility, majority of the farmers are equipped with tractor but agricultural equipment is insufficient, animal husbandry plays an important role for subsistence, and 64 % of the male farmers consult with the women for subsequent crop design (Tan, 2002).

Cereals

Wheat is the major field crop grown in Turkey with 7.529.639 ha, followed by barley with 2.748.766 ha. Average yield of these cereals are 2.670 and 2.580 kg/ha respectively (TÜİK, 2013). Both of these crops yield less than the average in high altitude marginal areas of Turkey which accounts for 55 % of total cereal production area. Assuming that landrace cultivation is associated with lower yield, wheat and barley landraces are grown at about 10% of the low yielding area, we end up with an area of 565.312 ha of wheat and barley landrace cultivation. There is no improved varieties in hulled wheat species and use of registered varieties in oats and rye is negligible. Total cultivation area of these crops are 3.988, 89.327 and 143.222 ha respectively. Altogether total cereal landraces cultivation area is estimated to be 801.849 ha which is 3,37% of all cultivation area. Wheat landraces are generally grown at small patches in west and northern transition zones of Central Plateau, forest openings of North Anatolia, Eastern and South eastern Anatolia. Besides the localized landraces, there are a few landraces grown in large areas such as *Tokak* (2 row barley), *Kunduru* (durum wheat) and *Köse* (bread wheat).

Wheat landraces of Turkey are usually kept as populations rather than selected homogenous cultivars. Thus those populations are characterized by great genetic and phenotypic variations. Thus landraces within a single village may show traits such as white, black or red grain; the presence and absence of awns; tightly or loosely packed spikes; and different abilities to tolerate abiotic conditions (Brush, 2004).

There are several records concerning emmer and einkorn cultivation in Turkey. Kobalyev (cited in Zhukovsky, 1951) who participated the expeditions conducted by Zhukovsky during 1925-1927 stated that "being a spring type of a crop of secondary importance, emmer cultivation area in Anatolia was about 2 % of all cultivated areas, and it is subject to total extinction in near future". Gökgöl (1939) reports that emmer was a low yielding type of wheat and it is being replaced by

higher yielding varieties. Today emmer and einkorn hulled wheat species are still being grown in sloping forest openings at the north transition area by very poor villagers for subsistence where no other crop can be grown. Altogether their acreage is about 3.988 ha which was 107.758 ha in 1948 (Karagöz, 1996; TÜİK, 2013). Local NGO's are working hard for introduction and spread of emmer. Emmer bulgur is now available in certain markets of big cities.

Sustainability of landraces

First thing to keep in mind is that loss of landraces is a continuous, irreversible event which is hard to cease. It is inevitable that landraces will continue to be replaced by genetically uniform cultivars. There may be ways of maintaining some of the landraces sustainably for long periods, but there seems to be no way of conserving all the landraces forever. Therefore it would be wise to concentrate on the most appropriate and promising ones rather than trying to keep entire variation. Suitable strategies for promising plant groups and regions must be very well identified.

There is no proven successful strategy for *in situ* conservation and sustainable use of landraces yet. Different strategies apply to different plant groups and target areas. Any conservation activity should take into consideration the socio economic conditions of the target groups. Flexible management plans, prepared for target species and target areas are needed. Plans should be prepared by participation of all possible stakeholders such as landrace producers, consumers, industry and exporters. Management plans should be flexible enough to keep up with the changing market demands. Promotion of market demand for the landraces should be one of the strategies of the plans.

Selecting target plant groups for *in situ* conservation of landraces is a critical issue and many factors are involved. Farmers would be interested in the species they are accustomed to, which are also the components of agricultural production system. Different or new crops may not be readily acceptable by the farmers. The key factor is that farmers are primary decision makers. Selection of target taxa should be left with the farmers. Where conservation of a species depends on maintenance of a particular ecosystem, due regard must also be paid to other species that are essential components of the ecosystem, even when these are not direct target of a conservation plan (Hawtin and Hodgkin, 1997). This is particularly the case where a certain rotation plan is applied. In

that case the other plant groups should also be taken into on farm conservation plans in rotation with the target species.

Suggestions for sustainability of landraces

It is hard to suggest something special for any of the target plants or regions for long term conservation. The key point here is that any agricultural activity is maintained if it is worth to do so. Any initiative should prepare the infrastructure to add value to landraces and try to convince the farmers that they will earn more if they do so. Farmers' participation is very important for success of the management plans. Below is a short list of suggestions; market creation, development of benefit sharing regimes for the farmers conserving landraces, conservation of traditional knowledge related with landrace utilization and conservation, development of on farm breeding facilities, growing landrace mixtures, amendment of seed registration system and/or creation of a special registry system for landraces and use of landraces in organic farming systems.

Creating new markets will have a positive impact on landrace cultivation. Consumers may not be aware of existence of new and different tastes and flavors that landraces bear. For example, there is a market in Italy for hulled wheat species and their products are sold at higher prices than ordinary wheat varieties, but in Turkey not many people are aware of existence of such varieties. Promotion of certain products made with landraces may create demand. For promotion of emmer production following points were recommended by Guiliani et al. (2009): "an active public awareness campaign targeted at consumers, to be put in place by local governments, with the involvement of nongovernmental organizations and farmers' organizations". The authors also appreciate the crucial role Policy-makers have in spreading information about the dietary benefits of emmer through the media, campaigns, and *ad-hoc* education programs.

Benefit sharing issue is one of the three principles of the Convention on Biological Diversity (CBD, 2008). Parties to the CBD agreed on Nagoya Protocol in 2010 to enable fair and equitable sharing of benefits arising from the utilization of genetic resources, thereby contributing to the conservation and sustainable use of biodiversity including landraces (Nagoya Protocol, 2013). The Nagoya Protocol is an agreement made in good faith among the parties which could only be beneficial for sustainable use

of landraces if it can be implemented in a fair manner within and among the countries.

Conservation of landraces is directly related with conservation and maintenance of traditional knowledge since landraces developed distinct feature under traditional system. Therefore it is of crucial importance that traditional knowledge is collected and maintained.

Selecting within landraces for desired characteristics poses a danger on their genetic diversity because it may result in highly heterogenous populations into genetically poor homogenous ones. On farm breeding option is still more preferable than replacing the landraces with high yielding cultivars since at least some of the genes and characteristics are maintained with this strategy.

Growing mixtures of landraces does apply for the ones with similar phenotypic characteristics. This strategy may be applied to the ones that are still being widely used like *Tokak* (barley), *Kunduru* (durum wheat). In case of highly mixed populations the same operation can be applied by selecting and mixing the similar types and returning them to the users in different lots. It may also add market value to the crop by having more homogenous product.

Existing seed certification system possesses problems to the landraces because of required homogeneity of the reproduction material. Although a number of landraces were released within this system in Turkey, they are all phenotypically homogenous because of eliminating off types among them for many years. Under strong restrictive seed certification systems the landraces have almost no chance to take market share. A less restrictive system allowing landraces to have diversity within the pre determined ranges is necessary.

It is also a fact that loss of landraces is associated with progress achieved in economic level and agricultural practices. Negative correlation between landrace cultivation and rural development suggest that, a way of integrating landrace cultivation into development plans should be searched. Social and economical progress provide new era for promotion of natural and healthy foods. People of the developed countries are more interested in consuming healthier food. This trend might be used for the benefit of landraces by integrating them into organic farming applications.

Being a production system which aims to reestablish the organic equilibrium of the ecological system, organic agriculture uses organic inputs at

limited level. Having a lot of varieties that are adapted to low input conditions, landraces provide invaluable source for organic farming practices. Landrace production areas are more suitable for organic farming because they are the least polluted parts of the farming systems. Potential of the landraces must be evaluated for their response to organic farming applications to provide new and varying sources to farmers and breeders.

Organic farms make use of large numbers of plant and animal species than conventional systems. As a result, the large pool of genetic resources for food and is maintained and other useful organisms such as predators, pollinators and other useful microorganisms are increased for the very benefit of the agricultural system.

There are several hundred millions of farmers in the world who do not have the economic means to buy high yielding seeds or synthetic fertilizers and pesticides, necessary for conventional cultivation. Many of these have opted for the maintenance or reintroduction of organic systems based on traditional forms of agriculture. These promote the use of varieties and breeds that are better adapted to local stress conditions and do not require unavailable and costly inputs.

There are also farmers who have opted for organic agriculture in part because they wish to produce healthy and environmentally friendly food, and also because they are attracted by the strong demand for organic products and related premium prices. Market driven farmers should, as minimum, rotate crops as the first step towards improving agricultural biodiversity. This is one of the methods required by organic certification bodies as well as by financial programs. These farmers have also opted for sowing locally adapted species and varieties that are more resistant to disease and local environmental conditions because synthetic fertilizers and pesticides cannot be relied upon (Sciallaba, 2003).

Organic crops cover a total of 614.618 ha in 2011 and number of organic products reached to 42.460 (TÜİK, 2013). Land and number of farmers dealing with organic agriculture tripled during 2005-2011. We can assume organic agriculture is a promising activity for Turkey for more widespread use and sustainability of landraces.

Conclusion

Landraces of wheat and other major and minor crops still play an important role in the livelihood of small scale farmers in Turkey. Several factors including physical, climatic, socio-economic, market facilities, and pricing policies, play a major

role in cultivation of landraces. It is estimated that cereal landraces cover almost 800.000 ha in Turkey. Loss of landraces is a continuous, irreversible event. It is inevitable that landraces will continue to be replaced by genetically uniform cultivars. There may be ways of maintaining some of the landraces sustainably for long periods, but there seems to be no way of conserving all the landraces forever. Market creation, development of benefit sharing regimes, conservation of traditional knowledge related with landrace utilization, development of on farm breeding facilities, growing landrace mixtures, ammdement of seed registration system and/or creation of a special registry system for landraces and use of landraces in organic farming systems are suggested for sustainability of crop landraces.

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REGULAR ARTICLE

Phenotypic and genotypic characterization of wheat landraces of Pakistan

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Abstract

Wheat landraces represent a large reservoir of genetic variation of various traits. In this study 28 entries from a collection of 40 maintained in AARI, Faisalabad initially collected from northern Pakistan (Khyber Pakhtunkhwa and Baluchistan) were evaluated for their genetic diversity using microsatellite (SSR) primers. The 40 entries comprised of landraces and earlier local cultivars (C numbers) with all possessing a spring growth habit. Major phonological and biotic stress passport data is on record. The morphological examination of these entries showed that those designated as T2, T3 (*Triticum durum*), T7 (*T. sphaerococcum*), T18 (*T. aestivum*) C-217 (C-516xC-591) and C-258 were agronomically elite as to plant habit. SSR primers amplified total 122 bands out of which 83 were polymorphic. The percentage of polymorphism was 68%. XGWM-337 and XGWM-194 were found to be highly polymorphic. T7, T12 (*T. aestivum*) and C-258 were found to be genetically most diverse landraces using the SSR markers. The polymorphism indicator and phenology profile are the basis for selecting from these germplasm for adding diversity to wheat breeding programs nationally.

Key words: *Triticum aestivum*, Landraces, Simple Sequence Repeats, Genetic diversity, Phenology

Introduction

Wheat (*Triticum* spp) is cultivated all over the world and the most important domesticated grass. In Pakistan, wheat is the major staple food of the people where 9.046 million hectares are covered by wheat having an average annual production equivalent to 24.032 million tons as documented by Hussain et al, (2011); which encompasses approximately 34% of the cultivated area of the country. The yield levels annually fluctuate due to outputs from the rainfed area with the 2012 May harvest touching 25mt at 2.6 tons/hectare. With the continuous increase in population, there is an ever-increasing demand for higher yield. A lot of

research is in place on bread wheat to maximize grain production per unit area. Most of the current cultivars in wheat do not exhibit a lot of genetic diversity rendering it vulnerable to various biotic stresses. There is, therefore, a great need to utilize sources of new diversity in breeding.

To tap on new diversity we have over the last 3 to 4 decades seen researchers exploit various Triticeae genera/species/accessions to widen the wheat genetic base via allelic enrichment using intra-specific, interspecific and intergeneric protocols (Mujeeb-Kazi et al., 2008; Mujeeb-Kazi et al., 2013; Ogbonnaya et al., 2013). There is general agreement that members residing in the primary gene pool occupy priority usage position since allelic transfers are based on homology and are swift. Within this framework access to diverse genomic variation is ample which imparts a solid genetic base to develop varieties that possess disease resistance durability options and a conduit to sustainable agriculture. Additive to the diversity framework are resources of the old varieties (pre-

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dwarfing types) and landraces extremely under-utilized but of huge significance value.

Since these landraces have developed through both natural and artificial selection (Belay et al., 1995), thus have a broader genetic base and can provide valuable contribution to breeding (Keller et al., 1991; Tesemma et al., 1998). These are proved to be a good source of tolerance to local stresses (Li et al., 1997) hence increase in yield (Tesemma et al., 1998).

There is always required a solid foundation about the level of genetic diversity available in crop germplasm for a good breeding program. The variation in agronomic, morphological and physiological traits show inaccurate genetic diversity due to environmental factor and polygenic traits. In addition, field evaluations are always tedious and labor-intensive.

The present study has addressed the phenotypic and genotypic characterization of 28 wheat landraces selected on seed abundance from a collection of 40 entries maintained in AARI, Faisalabad that were collected from the northern Pakistan areas of Khyber Pakhtunkhwa and Baluchistan and passport data generated in 2004-2005. The genotypic characterization will contribute in the parental selection in national breeding programs assisting the release of wheat varieties with better agronomic traits.

Material and Methods

This study was conducted on selected wheat landraces of Pakistan (Table 1).

Phenotypic variation

All landraces were grown in the field of National Agricultural Research Center (NARC), Islamabad. The data was taken for three plants from each accession and arithmetic means were calculated. The data was recorded for Pubescence, Plant height, Awn color, Physiological maturity, grain weight, number of grains per spike and spike length.

Genotypic analysis

Genomic DNA of 28 wheat land races of wheat was extracted following the method of Weining and Langridge (1991). DNA quantification was done through spectrophotometer.

SSR analysis

A total of 56 SSR primer pairs were utilized for DNA amplification using Polymerase Chain Reaction (PCR). Each PCR reaction consisted of 25-µl reaction mixture (11.3 µl d3 water, 2.5 µl 10X buffer, 2 µl MgCl₂, 2 µl dNTPs, 0.2 µl Taq polymerase, 1 µl of each primer of a primer pair, 5

µl DNA). The samples were incubated at 94°C for 4 min before 45 cycles (94°C for 1 min, primer annealing at 58-60°C for 1 min, extension at 72°C for 1 min). The final extension was done at 72°C for 10 min. The electrophoresis was done on 3% agarose gels with 7 µl of ethidium bromide at 80 V for 1 h to observe under UV transilluminator (Roder et al., 1998).

Table 1. Pedigree list of selected Landraces of Pakistan.

S. No.	Parentage/pedigree Sample detail	Data Information
1	T ₁ (<i>Triticum durum</i> ; 2n=4x=28)	AARI-T ₁
2	T ₂ (<i>T. durum</i> ; 2n=4x=28)	AARI-T ₂
3	T ₃ (<i>T. durum</i> ; 2n=4x=28)	AARI-T ₃
4	T ₇ (<i>T. sphaerococcum</i>)	AARI-T ₇
5	T ₈ (<i>T. aestivum</i> ; 2n=6x=42)	AARI-T ₈
6	T ₉ (<i>T. aestivum</i> ; 2n=6x=42)	AARI-T ₉
7	T ₁₂ (<i>T. aestivum</i> ; 2n=6x=42)	AARI-T ₁₂
8	T ₁₄ (<i>T. aestivum</i> ; 2n=6x=42)	AARI-T ₁₄
9	T ₁₅ (<i>T. aestivum</i> ; 2n=6x=42)	AARI-T ₁₅
10	T ₁₆ (<i>T. aestivum</i> ; 2n=6x=42)	AARI-T ₁₆
11	T ₁₇ (<i>T. aestivum</i> ; 2n=6x=42)	AARI-T ₁₇
12	T ₁₈ (<i>T. aestivum</i> ; 2n=6x=42)	AARI-T ₁₈
13	T ₂₀ (<i>T. aestivum</i> ; 2n=6x=42)	AARI-T ₂₀
14	T ₂₄ (<i>T. aestivum</i> ; 2n=6x=42)	AARI-T ₂₄
15	8A (selection) (<i>T. aestivum</i> ; 2n=6x=42)	AARI-8A
16	D-9 (Barani selection) (<i>T. aestivum</i> ; 2n=6x=42)	AARI-D9
17	C-217 (C-516 × C-591) (<i>T. aestivum</i> ; 2n=6x=42)	AARI-C217
18	C-228 (hard federation x 9D) (<i>T. aestivum</i> ; 2n=6x=42)	AARI-C228
19	C-245 (<i>T. aestivum</i> ; 2n=6x=42)	AARI-C245
20	C-247(<i>T. aestivum</i> ; 2n=6x=42)	AARI-C247
21	C-248 (<i>T. aestivum</i> ; 2n=6x=42)	AARI-C248
22	C-250 (<i>T. aestivum</i> ; 2n=6x=42)	AARI-C250
23	C-256 (<i>T. aestivum</i> ; 2n=6x=42)	AARI-C256
24	C-258 (<i>T. aestivum</i> ; 2n=6x=42)	AARI-C258
25	C-269 (<i>T. aestivum</i> ; 2n=6x=42)	AARI-C269
26	C-271 (C-220 x IP165) (<i>T. aestivum</i> ; 2n=6x=42)	AARI-C271
27	C-288 (<i>T. aestivum</i> ; 2n=6x=42)	AARI-C288
28	C-518 (T9 x 8A) (<i>T. aestivum</i> ; 2n=6x=42)	AARI-C518

Source: Dr. Aziz-ur-Rehman, AARI, Faisalabad (2004-2005).

Statistical analysis

The presence and absence of bands was scored as 1 and 0 respectively for cluster analysis of 28 genotypes using the Pop Gen software version 1.32 (Yeh et al., 2000) to calculate genetic diversity and similarity among genotypes.

Results

Phenotypic observations

The morphological data of 28 wheat landraces of Pakistan is summarized in Table 2.

SSR analysis

For the SSR analysis, total 15 chromosome specific primers were used. These primers amplified a total of 122 scorable bands ranging from 50bp to 500bp. Out of 122 scorable bands, 83 were polymorphic. SSR markers detected 68% of

polymorphism among the landraces (Figure 1). The highest number of allele was detected by XGWM-609 whereas XGWM 337 and XGWM-194 detected the highest level of polymorphism. The coefficient of similarities ranged from 40% to 95%. The lowest genetic similarity was found between T7 (*T. sphaerococcum*) with C-288 and T15 (*T. aestivum*) with C-288. The dendrogram analysis showed three main clusters. Cluster I included three genotypes with the genetic distance ranging from 0.08 (T1 and T2) to 0.32 (C-217). A total of 32 genotypes were included in cluster II. The genetic distance ranged from 0.05 (C-269, T18, T20) to 0.44 (T7). The cluster III included two genotypes. The genetic distance ranged from 0.64 (C-258) to 0.89 (T12).

Table 2. Phenotypic evaluation of 28 wheat landraces.

S. No.	Genotype	GC	PUB	FLOW	HT	AWN	P.MA	GWT	Nodes/ Spike	GR/Spike	Spikelng
1	T1	A1	-ive	130	106	B	145	32	12	47	8
2	T2	A1	-ive	130	112	W	144	31	12	36	8.7
3	T3	A1	-ive	129	108	LB	142	30	12	25	10.2
4	T7	A2	-ive	129	94	-	137	21	10	42	7.3
5	T8	A2	-ive	128	106	DB	137	30	8	34	8.2
6	T9	A2	-ive	127	104	DB	137	24	8	49	9.3
7	T12	A2	-ive	126	103	DB	145	25	7	79	9.6
8	T14	R2	-ive	123	99	LB	144	24	10	58	11
9	T15	R2	-ive	122	98	LB	145	26	10	34	11
10	T16	A2	-ive	128	104	LB	133	23	8	51	9.7
11	T17	A2	-ive	121	104	-	137	20	11	40	12.3
12	T18	A2	-ive	122	111	-	137	23	9	47	9.4
13	T20	A2	-ive	127	100	-	137	34	10	70	11.8
14	T24	A2	-ive	126	99	-	137	28	9	52	8.5
15	8A	A2	-ive	121	90	DB	144	29	11	31	8.8
16	D-9	A1	-ive	122	105	LB	140	29	9	47	10.2
17	C-217	A2	-ive	125	106	B	140	36	8	48	8.7
18	C-228	A2	-ive	119	111	B	144	31	9	45	9.8
19	C-245	A1	-ive	120	108	LB	144	30	9	45	8.7
20	C-247	A2	-ive	119	114	DB	144	30	10	55	8
21	C-248	A2	-ive	126	104	B	144	27	11	40	9.8
22	C-250	A2	-ive	128	102	LB	145	30	8	26	12
23	C-256	A2	-ive	124	100	LB	133	21	8	43	9.3
24	C-258	A2	-ive	125	85	-	133	37	7	29	8.8
25	C-269	A3	-ive	124	94	-	137	32	10	51	10
26	C-271	A2	-ive	119	113	B	137	41	10	55	10.4
27	C-288	A1	-ive	126	101	LB	137	33	10	46	7.5
28	C-518	A2	-ive	119	103	B	140	28	8	43	7.7

GC: Grain quality (A-Amber color; R-Red color; 1-Bold grain; 2-Medium grain; 3-Small, shrivelled grain); PUB: Pubescence; FLOW: Days to flowering; HT: Plant height at maturity; AWN: Awn color; P. MA: Days to physiological maturity; GWT: 1000 grain weight; NODES/SPIKE: Number of nodes per spike; GR/SPIKE: Number of grains per spike; SPIKELNG: Spike length.

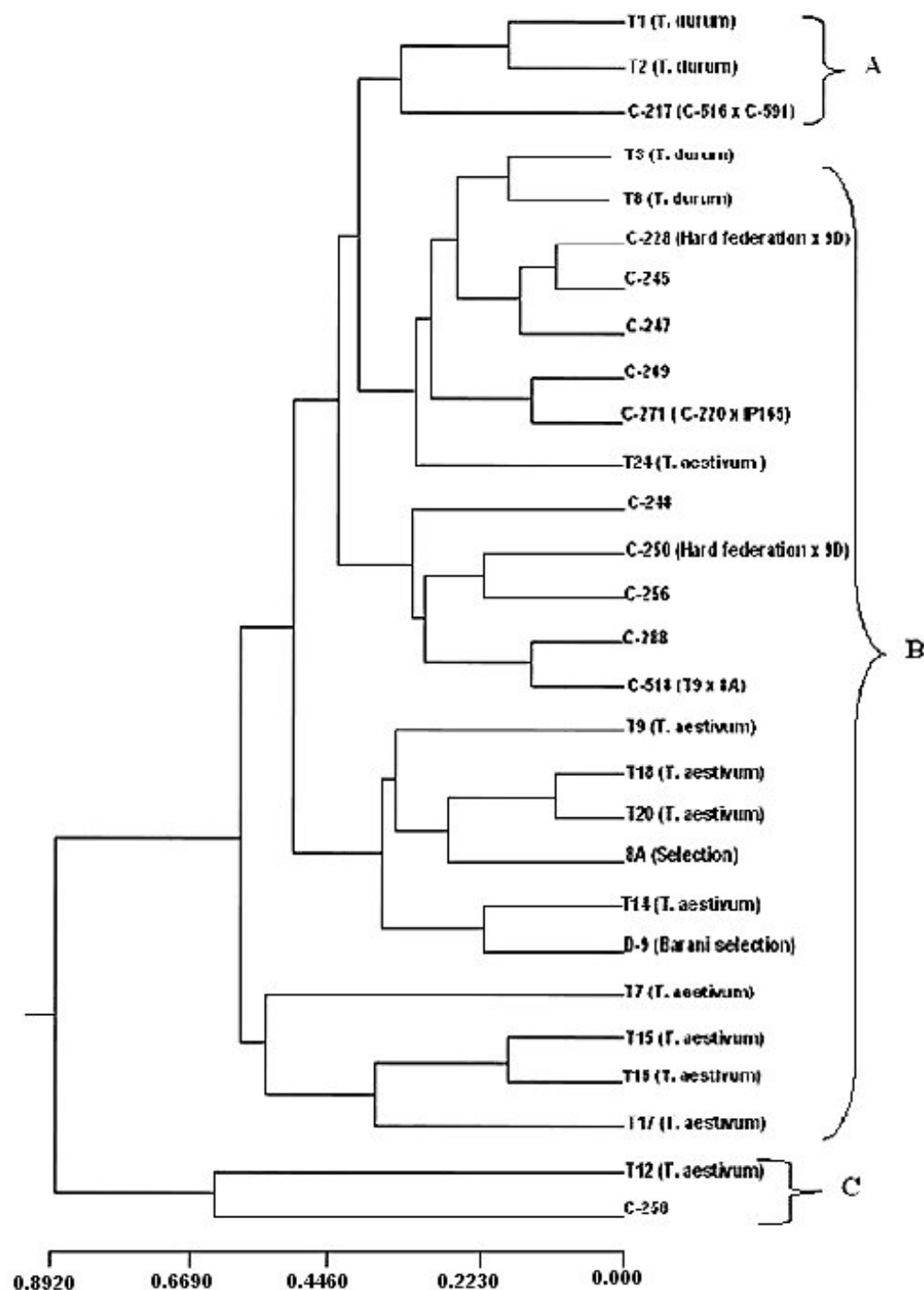


Figure 1. Cluster analysis of 28 wheat landraces using SSR primers.

Discussion

The landraces that have been cultivated around the world are especially important as a genetic resource because they have evolved adaptations to various environmental conditions. These landraces

have acquired this adaptation to diverse natural conditions due to natural selection and farmers' selection. They provide a good source of genetic diversity to various global breeding programs and are considered the most important genetic resource. Landraces have attracted the scientific community

due to their genetic variability in well-adapted backgrounds (Fathi et al., 2011). The study of genetic diversity provides important information about their breeding potential. Also, heterogeneity of wheat landraces is too complicated to analyze systematically (Nevo and Payne, 1987). For transgressive segregation, genetically diverse parents are mandatory (Joshi et al., 2004). Although, thousands of landraces are preserved in various seed banks of the world, the majority of these are insufficiently evaluated for exploitation in wheat breeding. The biochemical and molecular characterization have become a prerequisite for the modern seed industry. The evaluation of genetic diversity using molecular markers is an important tool in the effective management of genetic resources (Virk et al., 1995; Ford-Lloyd et al., 1997). SSR or microsatellites provide an efficient, rapid and reliable method for quality control in seed certification programs to identify the sources of seed contamination in order to maintain pure germplasm collection. SSRs are reproducible, co-dominant in inheritance hence multiallelic and comparatively abundant due to extensive genomic coverage (Plaschke et al., 1995; Fu et al., 2005; Gupta and Varshney, 2000; Achta et al., 2012).

This study was focused on the evaluation of genetic diversity of 28 genotypes of landraces using 15 SSR primers. The SSR primers generated a total of 122 alleles. The primer pair XGWM608 amplified maximum 8 bands whereas the minimum of 2 bands were amplified by the primer pair XGWM550. The highest level of polymorphism was detected by XGWM-337 and XGWM-194. This study confirmed the ability of microsatellite loci to reveal allelic diversity as already reported (Ravi et al., 2003; Ram et al., 2007). In this study the genotypes T2 (*T. durum*), T3 (*T. durum*), T4 (*T. spaeorococcum*), T18 (*T. aestivum*), C.217 (C-516 x C-519) and C-258 were the most diverse genotypes. These genotypes showed very good morphological characters as well.

Current observations exhibit a wide array of phenological and molecular polymorphism diversity. Both these variables provide selective sieves to target entries in pre-breeding programs. Height variations are indices of selections for irrigated and rainfed agriculture. Yield components (grains/spike, 1000 kernel weight) are integrated crucially with yield maximization targets and days to physiological maturity vital to combat climate change. We see variability for all aspects in the germplasm studied that gives us optimism to harness this novel diversity in a volatile manner.

Further it is fortuitous that another 700 landraces have been reported from the NARC genebank that will add further value to their exploitation after their stringent phenotyping together with genotyping assays based on GoldenGate (Chao et al., 2011), BeadExpress (Trebbi et al., 2011), Infinium platforms (Cavanagh et al., 2013) and 90K iSelect (Akhunov et al., 2013), or direct sequencing of populations through genotype-by-sequencing (GBS) approach (Davey et al., 2011; Poland et al., 2012).

Local genotypes provide a great source of alleles as multi locus combinations are suitable for different environment of each country (Allard, 1996). When diverse lines are utilized in breeding programs, there is more chance of transgressive segregation due to reshuffling of alleles by recombination resulting in high yielding genotypes (Sofalian et al., 2008). In addition, this high genetic variation can be used for effective gene tagging and genome mapping to pyramid genes for high yield, disease and insect resistance (Talebi et al., 2010).

Conclusion

The genetic structure of wheat land races is an evolutionary approach for survival and performance where combined effects of natural and human selection have orchestrated various suitable combinations of traits. This genetic diversity acts as a buffer against the outbreak of epidemics by delaying the formulation of new pathotypes. The development of new wheat varieties from land races is a practical strategy to improve the performance of crop in the farmers' field. These land races are the source of success for global breeding programs. This global effort to assemble and characterize these genetic resources is paramount for the world's fight against hunger.

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REGULAR ARTICLE

Morphological and agronomical characterization of common wheat landraces (*Triticum aestivum* L.) from the National Wheat Collection of Bulgaria

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Abstract

The knowledge about the extent of variability, the distribution and the relationship between descriptors within local germplasm collection are a high value for the improvement and the efficient genetic diversity maintenance and utilization of plant species. The objective of this study was to assess the morphological and agronomic characteristics of original germplasm of common wheat (*Triticum aestivum* L.), maintained in *ex situ* collection in IPGR-Sadovo. Fifty-five accessions of *Triticum aestivum* L. stored for more than 10 years in the National gene bank of IPGR-Sadovo were planted under field condition and their agro-morphological characters such as plant shape (at tillering), leaf-flag attitude (at the beginning of heading), spike attitude (at full ripeness), spike awnedness, spike color and spike shape, length of vegetative growth phase, plant height, length of spike, spikelets per spike and 1000 grain mass were recorded. The variation analysis showed that the most relative variable character during the period of study is the length of spike (C.V. %=15.09%), following to 1000 grain mass (C.V. %=8.04%) and spikelets per spike (C.V. %=7.66%). PC-analysis was applied to group accessions according to similarity on the basis of five traits (length of vegetative growth phase, plant height, spike length, spikelets per spike and 1000 seed weight) in two components in the factor plane. The analysis shows that the first component explains 30.349% of the total variation and the second -26.001%. Two factors explain total 56.350% of the variation in the experience. A database with assessment information of regenerated accessions was created. The results of this study will support efforts of conservation and utilization of landraces in winter bread wheat breeding programs.

Key words: Accessions, *Ex situ* conservation, Collection, Genetic resources, *Triticum aestivum* L.

Introduction

In the recent years increasingly recognize the importance of genetic resources on the prosperity of breeding selection, agriculture and ecology (Anonymous, 1999; Stoyanova et al., 1998). Narrowing the range of genetic variation observed in the common and durum wheat as a result of using of conventional breeding selection practices reducing the ability to improve productivity of crops (Hadjiivanova et al., 2010). By approaching the limits of biological productivity of wheat in the recent years has greatly increased the need of new initial material (Hailegiorgis, 2011; Graybosch and Peterson, 2010; Lanning et al., 2010). In this regard the formation of the current gene pool of wheat, its planned and targeted research has been and is a

major priority in the researching activity.

Collections of wheat as a genetic resource are maintained in the National Gene bank in the Institute of Plant Genetic Resources-Sadovo (12,539 accessions), (<http://eurisco.ecpgr.org>). The collections contain a large genetic diversity: local populations, breeding materials (mutants, hybrids, introduced cultivars and lines) and wild species originating from the country as well of all over the world (Odzhakova et al., 2007; Kolev and Stoyanova, 2005; Popova, 2003). The National collection of common wheat includes 9,591 accessions, from which 1,051 accessions originating from Bulgaria. The study of *ex situ* collections is done according the international descriptors lists (Anonymous, 1984). Comprehensive evaluation of collections is a major source of information to create a database with assessment information of plant genetic diversity (Kolev, 2001; Angelova and Popova, 1998). This assessment is carried out on a number of morphological and agronomical characteristics of the samples and ranges from 10 to 68 indicators depending on the type of culture and biology.

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The objective of this study was to assess the morphological and agronomic characteristics of original germplasm of common wheat (*Triticum aestivum* L.), maintained in *ex situ* collection in IPGR-Sadovo.

Materials and Methods

During the period 2010-2012 in the experimental field of Institute of Plant Genetic Resources-Sadovo are reproduced 55 accessions of common wheat (Table 1). All accessions originating from Bulgaria and characterized as “original germplasm” created in this region. The seeds been stored for more 10 year for long-term conservation under -18°C.

Sowings were made in the optimal time for this area: 10-15 October. Six rows were planted from each accession with row spacing 20/5 cm and 1 m

length. The standard variety –Sadovo1 was sown as a systematic check. Regular field management operations were performed during the cropping season.

Observations and evaluations of morphological, biological and agronomic traits were carried out according to international descriptors lists (Anonymous, 1984). The agronomic characters were taken after harvesting the plants. From each accession, 20 plants were collected for biometrical measurements.

Statistical analyses were performed using the statistical program SPSS 13.0. PC-analysis was applied to group accessions according to similarity on the basis of five traits (length of vegetative growth phase, plant height, spike length, spikelets per spike and 1000 seed weight) in two components in the factor plane.

Table 1. Inventory of local (native) *Triticum aestivum* L. accessions stored for more than 10 years in the National gene bank of IPGR-Sadovo.

No.	Accession number	Variety/ Line	No.	Accession number	Variety/ Line
1	1978-TRT-AE-122	2981-2988-3-2	29	1998-TRT-AE-17	KM-105
2	2000-TRT-AE-85	P-208	30	2000-TRT-AE-41	C-28
3	2000-TRT-AE-144	P-245	31	2000-TRT-AE-60	P-30
4	2000-TRT-AE-143	P-244	32	2000-TRT-AE-67	P-204
5	1978-TRT-AE-200	7285-8-1-7-4	33	2000-TRT-AE-97	P-154
6	1978-TRT-AE-203	7285-7-31-7-1-3	34	2000-TRT-AE-92	P-131
7	2000-TRT-AE-142	P-243	35	2000-TRT-AE-89	P-212
8	1980-TRT-AE-616	7293-3-41-4-5-1	36	2000-TRT-AE-84	P-126
9	1978-TRT-AE-199	7285-11-21-1-3-7	37	2000-TRT-AE-83	P-125
10	1997-TRT-AE-31	582	38	2000-TRT-AE-75	P-104
11	2000-TRT-AE-141	P-242	39	2000-TRT-AE-107	P-220
12	1998-TRT-AE-18	EI-106	40	2000-TRT-AE-111	P-172
13	2000-TRT-AE-35	C-17	41	2000-TRT-AE-113	P-183
14	2000-TRT-AE-40	C-27	42	2000-TRT-AE-121	P-229
15	2000-TRT-AE-42	C-31	43	2000-TRT-AE-127	P-235
16	2000-TRT-AE-49	C-46	44	2000-TRT-AE-128	P-187
17	2000-TRT-AE-50	C-47	45	2000-TRT-AE-129	P-190
18	2000-TRT-AE-102	P-215	46	2000-TRT-AE-145	P-246
19	2000-TRT-AE-101	P-214	47	2001-TRT-AE-295	BORIANA
20	2000-TRT-AE-100	P-213	48	2001-TRT-AE-296	JUNAK
21	2000-TRT-AE-98	P-159	49	1978-TRT-AE-157	SADOVO1
22	2000-TRT-AE-80	P-113	50	2001-TRT-AE-180	SADOVO 772
23	2000-TRT-AE-104	P-217	51	2000-TRT-AE-8	BONONIA
24	2000-TRT-AE-117	P-225	52	2000-TRT-AE-9	SADOVSKA BELIA
25	2000-TRT-AE-119	P-227	53	2000-TRT-AE-7	POBEDA
26	2000-TRT-AE-120	P-228	54	2000-TRT-AE-10	DIAMANT
27	2000-TRT-AE-130	P-191	55	1997-TRT-AE-1	MURGAVEC
28	1998-TRT-AE-16	EI-104			

Results and Discussion

Morphological characters

During the study, accessions were characterized by following morphological characters: plant shape (at tillering), leaf-flag attitude (at the beginning of heading), spike attitude (at full ripeness), spike awnedness, spike color and spike shape.

According to the plant shape investigated accessions were divided into 3 groups: semi-erect, drooping and strongly declined (Table 2). The largest numbers of accessions were with drooping plant shape (37 accessions) and strongly declined (17 accessions). Only one accession (2001-TRT-AE-296) was with semi erect plant shape (Table 2). The leaf-flag attitude of 45 accessions was semi-upright (15-45°) and upright (< 15°) at 7 accessions. Dominated the accessions with white color and cylindrical shape of spike and 39 accessions were without awns. In thirteen of them the lengths of the awns were less 21 mm. Only two accessions were with length of awns within the borders of 61-100 mm (2000-TRT-AE-235, 1997-TRT-AE-1).

According to the spike attitude accessions were grouped into 4 groups: erect, semi-erect, horizontal and nodding. The accessions with semi-erect attitude of spike were thirty and these with nodding attitude of spike only four (Table 2).

Agronomic characters

The biometrical measurements in this study included: length of vegetative growth phase, plant height, length of spike, spikelets per spike and 1000 grain mass (Table 3). The results show that the length of spike in the study varied from 5 to 11 cm. The highest values of this character (11 cm) were registered in 3 accessions (2000-TRT-AE-117, 2000-TRT-AE-113 and 2000-TRT-AE-84). The numbers of spikelets per spike were between 15 and 20. The mean value of plant height was 93.9 cm. Accessions with tall plants (90 to 100 cm) and heavy kernels (1000 grain mass from 36 to 40 g) dominated this set of accessions (Table 3). The length of vegetative growth phase (from growing to heading) varied from 183 to 187 days.

Table 2. Summary of morphological characters of 55 accessions of *Triticum aestivum* L.

Plant shape				
Groups	semi-erect (25-45°)	drooping (46-55°)	strongly declined (56-70°)	prostrate (>70°)
Total number of accessions	1	37	17	0
Leaf-flag-attitude				
Groups	semi-upright (15-45°)	horizontal (46-90°)	drooping (91-135°)	very drooping (>135°)
Total number of accessions	7	45	3	0
Spike-attitude				
Groups	Erect (<15°)	semi-erect (15-45°)	Horizontal (46-90°)	Nodding (91-135°)
Total number of accessions	2	30	19	4
Spike - shape				
Groups	pyramidal	cylindrical	clavate	fusiform
Total number of accessions	17	33	5	0
Spike-color				
Groups	white	red		
Total number of accessions	55	0		
Spike-awnedness				
Groups	absent	Awnless (<21 mm)	semi-awnes (21-60 mm)	Awned (61-100 mm)
Total number of accessions	39	13	1	2

Table 3. Biometrical descriptors of 55 accessions of *Triticum aestivum* L.

Plant height, cm		Spike lengt, cm		Spikelets per spike		1000 grain mass, g	
cm	Total number of accessions	cm	Total number of accessions	ns	Total number of accessions	g	Total number of accessions
<80	0	<6	1	<14	0	<30	0
80-90	17	6,1-8	22	15-17	28	31-35	22
91-100	36	8,1-10	29	18-20	27	36-40	29
>100	2	10,1-12	3	21-23	0	41-45	3
		>12	0	>24	0	46-50	1

The basic statistics of the main descriptive characteristics (mean, minimum and maximum, std.error of means, std. deviation, variance and coefficient of variation) of five characters are shown in Table 4. The values of coefficient of variation (C.V. %) are from 0.6 to 15.09 %. The analysis show that the most relative variable character during the period of study is the length of spike (15.09 %), following to 1000 grain mass (8.04 %) and spikelets per spike (7.66 %). The values of these coefficients confirm that these traits are more susceptible to change under the influence of different factors. Relatively the least variable for the period of study indicated the length of vegetative growth phase.

PC-analysis was applied to group accessions according to similarity on the basis of five traits (length of vegetative growth phase, plant height, spike length, spikelets per spike and 1000 seed weight) in two components in the factor plane. The values of the two components to each of the study parameters were calculated empirically (Table 5). The analysis shows that the first component explains 30.349 % of the total variation and the second -26.001 %. Two factors explain total 56.350 % of the variation in the experience. This relatively small percentage illustrated the existence of complex relationships between the studied characters. For example the characters: length of spike, number of spikelets per spike and 1000 grain mass are associated with the first component. The

second component is in correlation with length of vegetative growth phase and plant height (Figure 1).

The evaluation of phenotypic variability by multivariate analysis gives the possibility to include a large number of accessions and to identify the most suitable resources for special trait (Stoilova, 2007). Distribution of evaluated accessions in the coordinate system of PC1 and PC2, presents the grouping of accessions according to similarity of traits: length of vegetative growth phase, plant height, spike length, spikelets per spike and 1000 seed weight (Figure 2). Some of the accessions are separated as “detached” from other. The accession № 41 (2000-TRT-AE-113) in the upper right quadrant is characterized with least 1000 grain mass, long vegetative growth phase and largest length of spike. Sample № 46 (2000-TRT-AE-145) located to the opposite in the lower right quadrant is with largest number of spikelets of spike. The samples № 2, 3, 14, 49 (2000-TRT-AE-85, 2000-TRT-AE-144, 2000-TRT-AE-40 and 1978-TRT-AE-157) in the left lower quadrant are with the largest 1000 grain mass. The accessions №21 (2000-TRT-AE-98) and №5 (1978-TRT-AE-200) in the upper left quadrant are characterized with small length of spike and spikelets of spike and the bigger 1000 grain mass. These samples represent a certain interest to hybridization by different traits and can be recommended as donors in the breeding selection of winter bread wheat.

Table 4. The basic statistics of the main descriptive characteristics in accessions of *Triticum aestivum* L.

Parameters	Length of vegetative growth phase, days	Plant height, cm	Spike length, cm	Spikelets Per spike, ns	1000 grain mass, g
Mean	186.00	93.95	8.43	17.55	40.59
Std. Error of Mean	0.15	0.67	0.17	0.18	0.44
Std. Deviation	1.12	4.97	1.27	1.34	3.26
Variance	1.26	24.70	1.61	1.81	10.66
Minimum	183.00	80.00	5.00	15.00	31.80
Maximum	187.00	102.50	11.00	20.00	48.20
Coefficient of variation, %	0.60	5.29	15.04	7.66	8.04

Table 5. Weighted factors (PC1 and PC2) of descriptive characteristics on the rotated matrix with two factors.

Characters	PC 1	PC 2
Length of vegetative period, days	0.214	0.820
Plant height, cm	-0.162	0.815
Length of spike, cm	0.687	-0.140
Spikelets per spike, ns	0.561	0.013
1000 grain mass, g	-0.749	-0.205
% of total variance explained	30.345	26.001
Cumulative variation, %	30.345	56.350

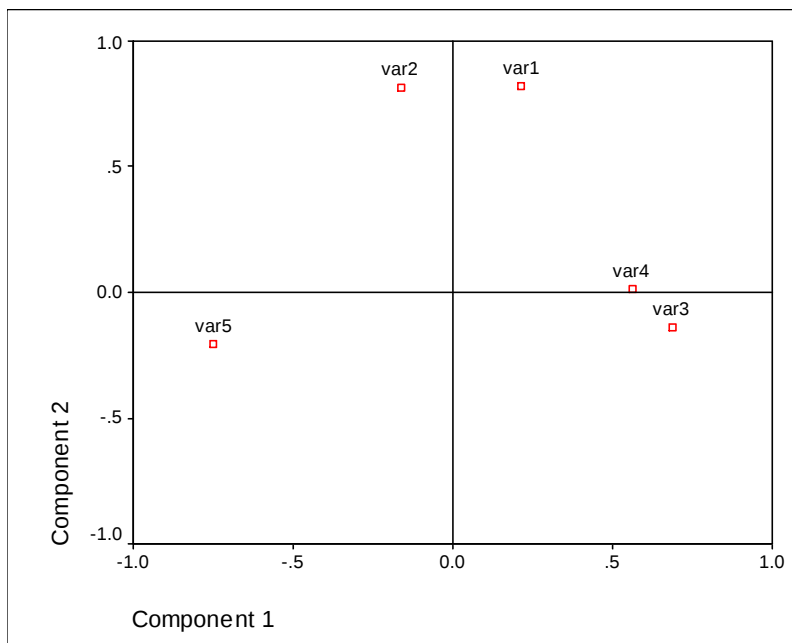


Figure 1. Projection of the traits on the factor plane (1 x 2): Length of vegetative growth phase, days (var1), Plant height, cm (var2), Spike length, cm (var3), Spikelets per spike (var4), 1000 grain mass, g (var5).

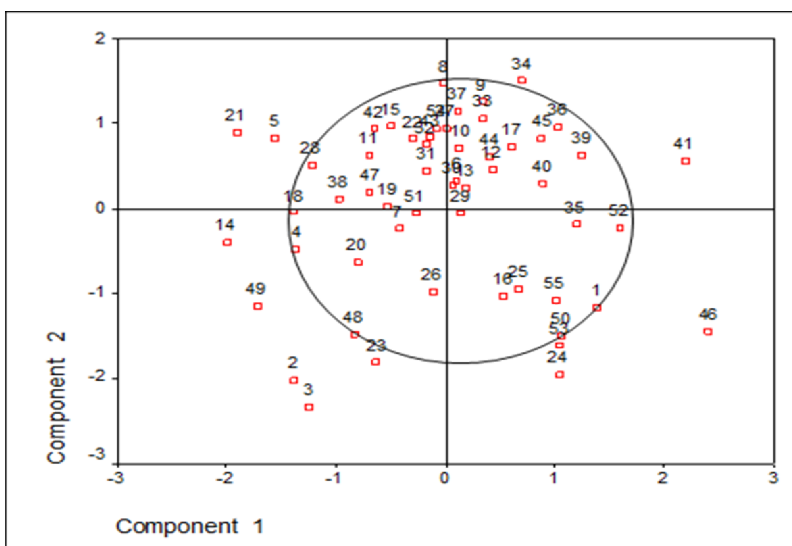


Figure 2. Distribution of evaluated accessions within the factor plane. The accessions presented with the conditional numbers 1-55 of the graph correspond to the description in Table 1.

Conclusion

The present research provided information on genotype studied and its grouping.

The most relative variable character during the period of study is the length of spike (C.V.-15.09%), following to 1000 grain mass (C.V.-8.04%) and spikelets per spike (C.V.-7.66%). Relatively the least variable for the period of study indicated the length of vegetative growth phase.

PC-analysis was applied to group accessions according to similarity on the basis of five traits in two components in the factor plane. The accessions: 2000-TRT-AE-145, 2000-TRT-AE-85, 2000-TRT-AE-144, 2000-TRT-AE-40 and 1978-TRT-AE-157 can be recommended as donors by different traits in the breeding selection of winter bread wheat.

A database with assessment information of investigated accessions in electronic format was created.

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REGULAR ARTICLE

Heat tolerance of Portuguese old bread wheat varieties

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Abstract

Wheat is a major staple crop, and its grain yield is affected by heat stress. Such environmental constraint frequently occurs in the main Portuguese wheat producing regions. The aim of this work was to evaluate the impact of high temperatures after anthesis on gas exchanges, chlorophyll a fluorescence, membrane integrity and yield in nine Portuguese old bread wheat varieties. Photosynthetic rate (Pn) reductions occurred in Gentil Rosso, Grécia and Nabão and may result from inactivation of PSII activity, as indicated by decreases in photochemical efficiency under light (Fv'/Fm') and in quantum yield of electron transport (ϕ_e). Results denoted an enhancement/maintenance of photosynthetic ability under heat, expressed by stable stomatal conductance (gs) and higher water use efficiency (WUE) in MEQ and Restauração, increased Pn in MEB and Restauração, and Pn stability in Ruivo. Reduced membrane damage (lower leakage) in Ruivo and MEQ suggested a higher protoplasmic tolerance to heat in these varieties. Control plants of MEQ also presented the highest lipid amount and the less unsaturated membrane lipids (low double bond index), and these traits were unaffected by heat. Ruivo denoted a stimulation of lipid biosynthesis which could have positive implications on thermal tolerance. Increased Pn and WUE, stable gs and abundant lipids in control plants (MEQ, T94, MEB, Restauração) corresponded to kernel yield increases under heat. Physiological traits are expected to contribute to Portuguese wheat breeding programs towards high temperature tolerance.

Key words: High temperature, Photosynthetic activity, Membrane integrity, *Triticum aestivum*, Yield

Introduction

Wheat is a staple food for more than 35% of the world population. It is also one of the main grain crops in Portugal. South Portugal (Alentejo) is an important wheat producing region, characterized by Mediterranean climate conditions, where increasing water stress associated with high temperatures become more frequent and reduce crops yield (Maças, 1996). Mean daily temperature of 15°C is considered optimal for wheat development (Chowdhury and Wardlaw, 1978), but above this threshold a reduction in the duration of grain filling period is observed (Al-khatib and Paulsen, 1984). In Alentejo, mean daily temperatures above 15°C,

and maximal temperatures above 32°C, are frequent during grain filling period (March to the end of June). Abiotic stresses such as drought and heat are predicted to occur more frequently due to climate change (Arnell, 1999). Wheat grain production depends on successful reproductive development (Wang et al., 2012), and the selection of adequate genotypes to face such environmental constraints may contribute to mitigate stress impact on productivity. Wheat genetic breeding programs in Alentejo have been concerned with heat tolerance traits among others (Maças, 1996; Barradas et al., 1996; Almeida, 2007).

Ecophysiological traits are useful to assess plant responses to environmental changes (Campos et al., 1999; Ramalho et al., 1999; Shvaleva et al., 2008; Matos et al., 2009). Under high temperature conditions, photosynthetic rates measured during grain filling have been positively associated with yield (Quinn and Williams, 1985; Reynolds, 1998; Erdei et al., 2002). High temperatures may damage plant cell membranes resulting in photosynthesis reductions. Heat stress induces the production of

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reactive oxygen species, which can bring about peroxidation of membrane lipids, leading to membrane injury (Blum and Ebercon, 1981; Almeselmani et al., 2006; Leshem, 1992), photosynthesis impairment and leaf senescence (Zhao et al., 2007). As observed for other stressful conditions, the ability to maintain membrane integrity and, hence, cell compartmentalization and metabolism, is crucial for plants survival under heat stress. That relies, mostly, on the dynamics of the lipid matrix of cellular membranes, which includes quantitative and qualitative modifications upon stress exposure (Matos et al., 2002; Dias et al., 2010; Scotti-Campos et al., 2011).

The aim of this work was to evaluate photosynthetic performance and membrane integrity in nine old Portuguese bread wheat varieties subjected to high temperatures after anthesis, under greenhouse controlled conditions. Evaluation was based on leaf gas exchanges, chlorophyll *a* fluorescence, membrane integrity and yield. Characterization of heat tolerance responses is expected to contribute to breeding programs aiming at a better adaptation of future wheat varieties to warm environments.

Materials and Methods

Seeds from 7 old Portuguese wheat varieties, were used in this study. These were: Gentil Rosso (G. Rosso), Grécia, Mocho de Espiga Branca (MEB), Mocho de Espiga Quadrada (MEQ), Restauração (Restaur.), Ruivo, Transmontano 94 (T94). These varieties were previously selected from a wheat germplasm (Vasconcelos 1933) belonging to INIAV. Two commercial varieties (Ardila, Nabão) were also sown in order to allow a comparison with currently used cultivars. Sowing took place in December in a greenhouse (INIAV/Oeiras) with controlled temperature conditions, in 7 L pots. These were filled with clay loam soil collected from the field (Lisbon), mixed with 20 g of granular fertilizer (Blaukorn, Bayer, N:P:K:micronutrients, 12:12:17:2). Four pots were used for each genotype, with a sowing density of 7 seeds per pot and 2.5 cm depth. Temperature, relative air humidity and radiation were monitored by means of two data loggers (Mezão Lda., Portugal). Diurnal maximal temperature and relative humidity varied between 23-26 °C and 50-60 %, respectively, along the experimental period. Natural irradiation ranged from 400 to 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ along the day inside the greenhouse.

Fourteen days after sowing (DAS) germinated seeds were thinned to five plants per pot, tillers were removed along development and the plants

were well watered throughout the growing period. Ten days after visual assessment of anthesis (during the grain filling period, 3.5 months old plants), which corresponded to different dates according to varieties, two pots of each genotype were left under control conditions while the two remaining pots were placed in a different greenhouse compartment. The heat stress treatment consisted in the plant exposure to maximal temperatures *ca.* 10 °C higher than the control (reaching *ca.* 40 °C, during 4 h each day, for 7 days). Watering was maintained in both compartments, to avoid RWC lowering of heat exposed plants. At the end of the high temperature imposition, measurements were performed in adult flag leaves and pots returned to the compartment under control conditions. Plants were allowed to continue until full maturation (*ca.* 150 DAS), and were individually harvested.

Leaf gas exchanges

The evaluation of net photosynthetic rate (P_n), stomatal conductance (g_s), transpiration (E) and water use efficiency (WUE) was performed during the morning period (10:00-12:00), using a portable $\text{CO}_2/\text{H}_2\text{O}$, infrared gas analyzer exchange system LI-6400 (LI-COR Inc., Lincoln, USA), with an external CO_2 concentration of *ca.* 370 $\mu\text{L L}^{-1}$, chamber block temperature controlled at 25°C, and artificial light adjusted at 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ supplied by a “cold” lamp LED type. The parameters were calculated according to the equations of Caemmerer and Farquhar (1981). The sensor head encloses a leaf surface of up to 6 cm^2 , well stirred to minimize boundary layer resistance as referred by Matos et al. (1998). For each parameter, the mean value of three measurements (minimum) is presented.

Chlorophyll *a* fluorescence

Diurnal Chl *a* fluorescence parameters were determined immediately after gas exchange measurements, under the same environmental conditions, using a PAM 2000 system (H. Walz, Effeltrich, Germany), as described in Ramalho et al. (2003), following the formulae reported elsewhere (Krause and Jahns, 2004; Schreiber, 2004). Briefly, the maximal PSII efficiency of energy conversion under light (F_v'/F_m'), the estimate of the quantum yield of non-cyclic electron transport (ϕ_e) and the photochemical quenching (q_p), which denotes the proportion of energy trapped by PSII and driven to photochemical events, were obtained under photosynthetic steady-state conditions, using a PPFD of *ca.* 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of actinic light (provided by a halogen lamp from the PAM-2000)

and superimposed saturating flashes (of ca. 7000 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

Electrolyte leakage

For each variety, four leaves (one per plant) were cut into 1 cm^2 sections. Pooled samples of 7 leaf sections (three replicates per treatment) were floated on 10 mL of deionized water for 22 h. Conductivity values resulting from electrolytes released by cells were read using a conductimeter Crison GLP 31 (Crison Instruments, Spain), at ca. 20°C. Total conductivity was measured after sample exposure to 90°C in an oven for 2 h, followed by cooling. Membrane leakage was expressed as a percentage of the total conductivity.

Lipid analysis

Lipid analysis was performed as earlier described in Campos et al. (2003). For each variety, four leaves (one per plant) were cut into 1 cm^2 sections, and pool samples (ca. 1 g FW, three replicates per treatment) were boiled for 2 min in distilled water to stop lipolytic activities. Total lipids were extracted in a mixture of chloroform/methanol/water (1/1/1, by vol.) according to Allen et al. (1966). For fatty acids (FAs) analysis, aliquots of total lipids extract were saponified and methylated with BF_3 -methanol (Merck), using heptadecanoic acid (C17:0) as internal standard (Metcalfe et al., 1966). Two methylation replicates were performed for each extract.

The fatty acid methyl esters were analysed with a gas-liquid chromatograph (Varian, CP-3380, USA) equipped with a flame-ionization detector. Separation was carried out on a capillary DB-Wax column (J & W Scientific, 0.25 mm i.d. x 30 m, 0.25 μm), as described in Campos et al. (2003). Column temperature was programmed to rise from

80°C to 200°C at a rate of 12°C min^{-1} , after 2 min at the initial temperature. Injector and detector temperatures were 200°C and 250°C, respectively. Carrier gas was hydrogen with a flow rate of 1 ml min^{-1} , at a split ratio of 1:100 of the sample. Fatty acids were identified by comparison with known Sigma standards. The value for the total fatty acids (TFA) corresponds to the sum of individual FAs. The unsaturation degree of TFA was obtained through a double bond index (DBI), calculated according to the formula: $\text{DBI} = [(\% \text{monoenes} + 2 \times \% \text{dienes} + 3 \times \% \text{trienes}) / \% \text{saturated FAs}]$ (Mazliak, 1983).

Grain yield

Plants were individually harvested at full maturity (ca. 150 DAS) and threshed manually after oven drying of the shoots at 35°C for 72 h. Grain yield (kernel weight per plant) was determined.

Statistical analysis

A two-way ANOVA ($P < 0.05$) was applied, using Statistix 9 (Analytical Software, 2009), followed by a Tukey test for mean comparison (95% confidence level).

Results

Plant water status and gas exchanges

As regards net photosynthesis (P_n), Nabão and MEB presented the highest and the lowest absolute values (14.5 and 9.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively), under control conditions (Figure 1). Heat stress induced significant P_n decreases in MEQ, Gentil Rosso, Transmontano 94, Ardila, Grécia and Nabão (24%, 18%, 14%, 12%, 10% and 5%, respectively), whereas P_n remained unaltered in Ruivo, and increased in MEB (36%) and Restauração (8%).

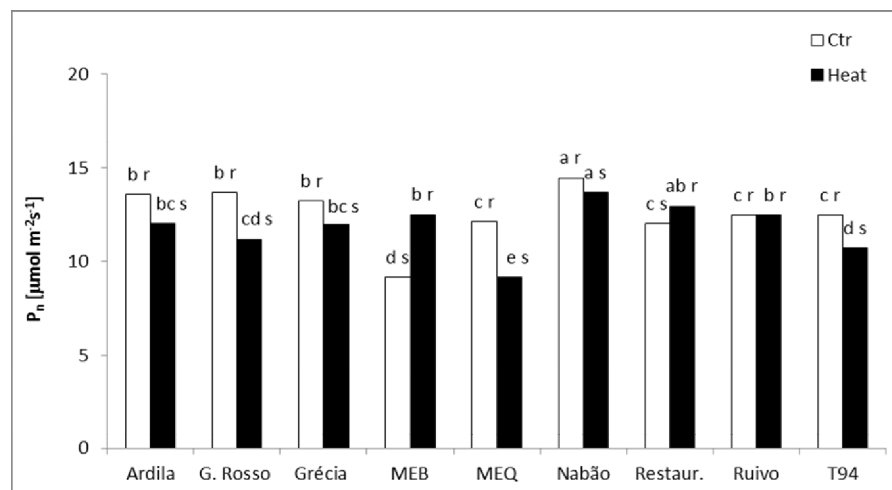


Figure 1. Changes in net photosynthesis (P_n) in leaves of nine *T. aestivum* genotypes, under control (Ctr) or heat conditions imposed after anthesis. Different letters express significant differences between genotypes for each treatment (a, b, c, d, e) or between control and heat treatment for the same genotype (r, s).

Ruivo presented the highest g_s in control plants, whereas the lowest value was found in MEB ($136.3 \mu\text{mol m}^{-2} \text{s}^{-1}$). However, the latter presented the highest rise (165%), to $361.4 \mu\text{mol m}^{-2} \text{s}^{-1}$, after heat exposure (Table 1). High temperature also induced significant g_s increases in Nabão (116%), Ardila (85%) and Grécia (61%), whereas the other genotypes maintained values close to their respective controls.

Accordingly to the highest g_s rise amongst genotypes, MEB presented also the highest transpiration (E) increase (346 %). Increases in E also occurred in all other genotypes (ranging from 207% in Grécia to 20 % in Ruivo) except MEQ and Restauração, what is in accordance with their stable g_s values. As regards internal CO_2 (C_i), a decrease was observed only in Restauração (26%). Small increases were observed in Ruivo (7%) and Gentil Rosso (4%). In all the others C_i increased (from 32 to 55%), being maximal raises observed for MEB (Table 1). Water use efficiency (WUE) increased in MEQ and Restauração (85% and 65%, respectively), whereas all the others genotypes showed WUE reductions (Table 1), particularly in the case of MEB and Nabão (68-70% decreases).

Chlorophyll a fluorescence

In control plants, Ardila and Ruivo showed the lowest PSII photochemical efficiency (F_v'/F_m') and photosynthetic electron transport (ϕ_e) values (Table 2). After high temperature imposition, a significant decrease of F_v'/F_m' occurred in Gentil Rosso (28%), Grécia (18%) and Nabão (12%). MEQ, Restauração, Ruivo and Transmontano 94 revealed only non-significant decreases, whereas Ardila and MEB showed to be completely unaffected. Quite similar variations were found for ϕ_e , namely in the reductions of 31%, 24% and 11% showed by Gentil Rosso, Grécia and Nabão, respectively. As regards the photochemical quenching (q_p), no differences were found between genotypes under control. Furthermore this parameter was unaffected by heat in all genotypes (Table 2), except in Grécia that presented a 6.5% drop.

Electrolyte leakage

Under control conditions, the lowest electrolyte leakage was obtained in Ardila, Nabão and Restauração, whereas Ruivo presented the highest membrane leakage (Figure 2). Heat stress did not promote an increase in membrane permeability in none of the genotypes, with significant reductions being observed in MEQ and Ruivo.

Table 1. Changes in stomatal conductance (g_s), transpiration (E), internal CO_2 concentration (C_i) and water use efficiency (WUE) in leaves of nine *T. aestivum* genotypes under control (Ctr) or heat conditions imposed after anthesis.

Genotype	Treatment	g_s	E	C_i	WUE
		$\text{mmol m}^{-2} \text{s}^{-1}$	$\text{mmol m}^{-2} \text{s}^{-1}$	$\mu\text{mol mol}^{-1}$	P_n / E
Ardila	Ctr	176.9 ^{cs}	3.4 ^{bc s}	232.4 ^{cs}	4.1 ^{cr}
	Heat	326.7 ^{bc r}	7.9 ^{br}	306.4 ^{br}	1.6 ^{ds}
G. Rosso	Ctr	171.8 ^{cr}	3.9 ^{as}	236.0 ^{cs}	3.6 ^{de r}
	Heat	184.4 ^{dr}	6.7 ^{cr}	244.9 ^{er}	1.7 ^{cd s}
Grécia	Ctr	193.0 ^{bc s}	3.3 ^{cd s}	249.8 ^{bs}	4.2 ^{cr}
	Heat	310.6 ^{cr}	10.0 ^{ar}	301.8 ^{bc r}	1.2 ^{ds}
MEB	Ctr	136.3 ^{ds}	1.5 ^{fs}	186.7 ^{ds}	6.0 ^{ar}
	Heat	361.4 ^{br}	6.9 ^{cr}	289.5 ^{bc r}	1.9 ^{cd s}
MEQ	Ctr	222.3 ^{br}	3.3 ^{bc r}	188.8 ^{ds}	3.7 ^{ds}
	Heat	218.1 ^{dr}	3.5 ^{dr}	285.5 ^{cr}	6.9 ^{ar}
Nabão	Ctr	225.2 ^{bs}	3.0 ^{des}	245.6 ^{bc s}	6.3 ^{br}
	Heat	486.9 ^{ar}	7.2 ^{bc r}	330.8 ^{cr}	1.9 ^{cd s}
Restaur.	Ctr	187.9 ^{bc r}	3.7 ^{abr}	254.9 ^{br}	3.5 ^{des}
	Heat	211.6 ^{dr}	3.4 ^{er}	189.2 ^{fs}	5.8 ^{br}
Ruivo	Ctr	303.6 ^{ar}	3.8 ^{as}	281.2 ^{as}	3.5 ^{er}
	Heat	319.0 ^{cr}	4.7 ^{dr}	301 ^{bc r}	2.7 ^{cs}
T94	Ctr	220.1 ^{br}	2.9 ^{es}	188.1 ^{ds}	4.2 ^{cr}
	Heat	225.0 ^{dr}	6.4 ^{cr}	268 ^{dr}	2.0 ^{cd s}

Different letters express significant differences between genotypes for each treatment (a, b, c, d, e) or between control and heat treatment for the same genotype (r, s).

Table 2. Changes in photochemical efficiency of PSII under photosynthetic steady-state conditions (F_v'/F_m'), quantum yield of photosynthetic electron transport (ϕ_e) and photochemical quenching (q_p) in leaves of nine *T. aestivum* genotypes under control (Ctr) or heat conditions imposed after anthesis.

Genotype	Treatment	F_v'/F_m'	ϕ_e	q_p
Ardila	Ctr	0.394 ^{br}	0.351 ^{br}	0.891 ^{ar}
	Heat	0.407 ^{ar}	0.357 ^{ar}	0.866 ^{ar}
G. Rosso	Ctr	0.458 ^{abr}	0.414 ^{abr}	0.904 ^{ar}
	Heat	0.328 ^{as}	0.284 ^{as}	0.866 ^{ar}
Grécia	Ctr	0.486 ^{abr}	0.445 ^{abr}	0.916 ^{ar}
	Heat	0.396 ^{as}	0.338 ^{as}	0.857 ^{as}
MEB	Ctr	0.420 ^{abr}	0.344 ^{abr}	0.823 ^{ar}
	Heat	0.427 ^{ar}	0.388 ^{ar}	0.910 ^{ar}
MEQ	Ctr	0.565 ^{ar}	0.509 ^{ar}	0.901 ^{ar}
	Heat	0.516 ^{ar}	0.478 ^{ar}	0.927 ^{ar}
Nabão	Ctr	0.487 ^{ar}	0.432 ^{abr}	0.885 ^{ar}
	Heat	0.430 ^{as}	0.383 ^{as}	0.890 ^{ar}
Restaur.	Ctr	0.533 ^{ar}	0.399 ^{abr}	0.746 ^{ar}
	Heat	0.498 ^{ar}	0.374 ^{ar}	0.751 ^{ar}
Ruivo	Ctr	0.335 ^{br}	0.290 ^{br}	0.859 ^{ar}
	Heat	0.306 ^{ar}	0.256 ^{ar}	0.836 ^{ar}
T94	Ctr	0.399 ^{abr}	0.337 ^{abr}	0.845 ^{ar}
	Heat	0.330 ^{ar}	0.299 ^{ar}	0.904 ^{ar}

Different letters express significant differences between genotypes for each treatment (a, b, c, d, e) or between control and heat treatment for the same genotype (r, s).

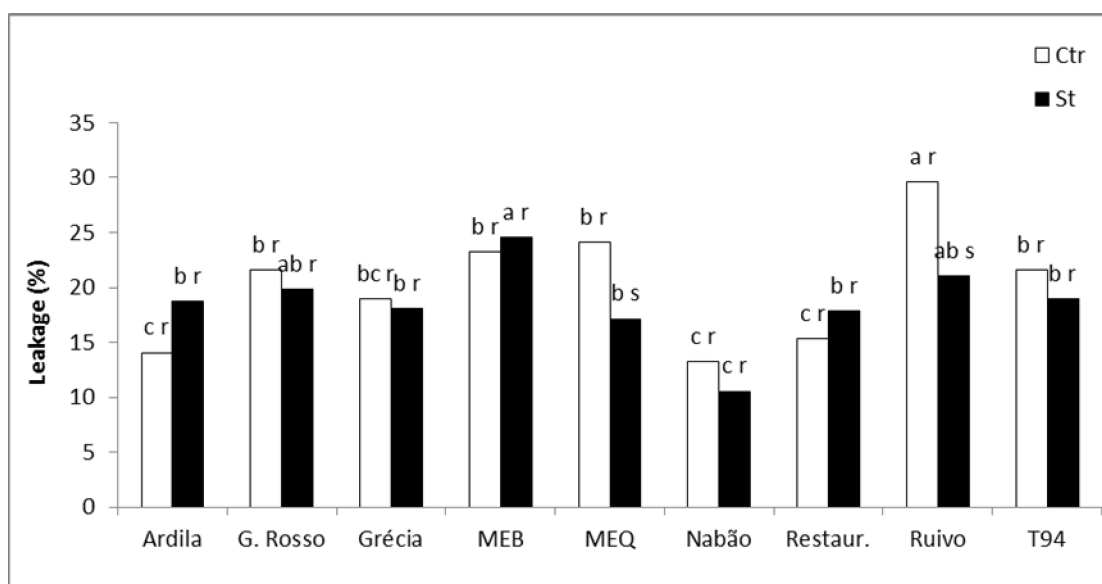


Figure 2. Changes in electrolyte leakage values in leaf sections of nine *T. aestivum* genotypes, under control (Ctr) or heat conditions imposed after anthesis.

Different letters express significant differences between genotypes for each treatment (a, b, c, d, e) or between control and heat treatment for the same genotype (r, s).

Lipid analysis

As regards total fatty acids (TFA), under control conditions (Table 3) the highest contents were observed in Transmontano 94 and MEQ (ca. 19-20 mg g⁻¹ DW), followed by MEB (15 mg g⁻¹ DW) and Restauração (13.5 mg g⁻¹ DW). The lowest TFA content was found in Ruivo (5.2 mg g⁻¹

DW), Ardila (7 mg g⁻¹ DW) and Grécia (9 mg g⁻¹ DW). After heat treatment no significant differences were found in lipid amounts except for Ruivo, where a 100% increase was observed (Table 3).

Concerning the individual fatty acids (FA), in control plants linolenic acid (C18:3) was by far the

most abundant FA, followed by palmitic (C16:0), linoleic (C18:2) and palmitoleic (C16:1) acids (Table 3). After high temperature exposure, plants presented a stable FA composition in relation to control. The only significant changes were found for T94 (decrease of C18:3 and increase of minor FA), Ruivo and MEB (lower and higher C16:0, respectively).

As regards TFA unsaturation degree, the heat treatment did not significantly influence the double bond index (DBI). However, lower DBI values occurred in MEQ and Transmontano 94, both under control and after high temperature exposure, indicating higher membrane FA saturation in these two cultivars (Table 3). In both the unsaturated palmitic acid (C16:0) was clearly more abundant (30-37%) than in the remaining cultivars (13-17%),

regardless of treatment. Furthermore the highly unsaturated linolenic acid (C18:3) was found in lower percentages in MEQ, and decreased in Transmontano 94 after heat treatment.

Grain yield

High temperatures induced an increase (>10% in relation to control) in grain yield (kernel production per plant) in MEQ (38%), Nabão (18%), Transmontano 94 (18%), and MEB (12%) (Figure 3). Gentil Rosso and Restauração presented small positive variations, whereas the remaining genotypes showed negative yield impacts, with decreases of 13%, 20% and 21% in Grécia, Ruivo e Ardila, respectively.

Table 3. Changes in fatty acid composition (mol %), total fatty acids (TFA) content and unsaturation (DBI) of total lipids in leaves of nine *T. aestivum* genotypes under control (Ctr) or high temperature conditions imposed after anthesis. Different letters express significant differences between genotypes for each treatment (a, b, c, d, e) or between control and heat treatment for the same genotype (r, s).

		<16:0	16:0	16:1 c+t	18:0	18:1	18:2	18:3	TFA mg g ⁻¹	DBI
		mol %								DW
Ardila	Ctr	10.9 ^{br}	14.8 ^{cr}	4.7 ^{ar}	2.4 ^{ar}	1.8 ^{br}	9.6 ^{bc r}	55.8 ^{bc r}	7.1 ^{dr}	11.4 ^{ab r}
	Heat	9.2 ^{cd r}	13.0 ^{br}	5.7 ^{ar}	2.8 ^{br}	2.3 ^{br}	8.1 ^{er}	58.9 ^{ar}	7.6 ^{er}	13.0 ^{ar}
G. Rosso	Ctr	6.7 ^{cr}	14.2 ^{cr}	2.6 ^{br}	1.4 ^{bc r}	1.4 ^{br}	10.5 ^{bc r}	63.3 ^{ar}	10.7 ^{cr}	13.9 ^{ar}
	Heat	9.38 ^{cr}	15.0 ^{br}	2.1 ^{cr}	1.3 ^{de r}	2.3 ^{br}	11.5 ^{cd r}	57.9 ^{ar}	10.3 ^{dr}	12.7 ^{ar}
Grécia	Ctr	6.8 ^{cr}	13.5 ^{cr}	1.9 ^{br}	1.9 ^{br}	1.7 ^{br}	9.4 ^{cd r}	64.8 ^{ar}	8.7 ^{dr}	14.5 ^{ar}
	Heat	8.9 ^{cd r}	14.0 ^{br}	3.4 ^{br}	2.2 ^{bc r}	2.0 ^{bc r}	11.5 ^{cd r}	58.0 ^{ar}	10.4 ^{dr}	12.7 ^{ar}
MEB	Ctr	4.3 ^{cd r}	17.1 ^{cr}	2.0 ^{bs}	1.1 ^{bc r}	1.7 ^{br}	14.4 ^{ar}	59.5 ^{ab r}	14.7 ^{br}	11.7 ^{ab r}
	Heat	3.9 ^{er}	16.6 ^{br}	3.0 ^{cr}	0.9 ^{er}	1.4 ^{cr}	15.8 ^{ar}	58.3 ^{ar}	14.9 ^{br}	13.1 ^{ar}
MEQ	Ctr	12.5 ^{ab r}	37.2 ^{ar}	2.4 ^{br}	1.9 ^{br}	1.7 ^{br}	15.0 ^{ar}	29.3 ^{dr}	19.2 ^{ar}	3.2 ^{cr}
	Heat	13.7 ^{br}	31.2 ^{ar}	2.7 ^{cr}	1.9 ^{cd r}	1.8 ^{bc r}	12.7 ^{bc r}	36.0 ^{cr}	19.5 ^{ar}	4.2 ^{br}
Nabão	Ctr	5.5 ^{cr}	14.3 ^{cr}	4.8 ^{ar}	1.3 ^{bc r}	1.4 ^{br}	13.3 ^{ar}	59.3 ^{ar}	10.9 ^{cr}	13.9 ^{ar}
	Heat	6.7 ^{de r}	16.1 ^{br}	4.4 ^{br}	2.2 ^{bc r}	1.6 ^{bc r}	13.1 ^{abc r}	55.9 ^{ab r}	12.7 ^{cr}	10.9 ^{ar}
Restaur.	Ctr	2.1 ^{dr}	16.1 ^{cr}	5.1 ^{ar}	1.0 ^{cr}	1.1 ^{br}	12.2 ^{ab r}	62.3 ^{ab r}	13.5 ^{br}	12.8 ^{ab r}
	Heat	4.8 ^{er}	16.8 ^{br}	5.6 ^{ar}	2.0 ^{bc r}	1.7 ^{bc r}	15.1 ^{ab r}	54.1 ^{ab r}	11.6 ^{cd r}	10.8 ^{ar}
Ruivo	Ctr	15.1 ^{ar}	16.4 ^{cr}	4.3 ^{ar}	3.0 ^{ar}	2.7 ^{ar}	6.7 ^{ds}	51.7 ^{cr}	5.2 ^{es}	10.2 ^{br}
	Heat	16.5 ^{ar}	12.9 ^{br}	2.3 ^{cs}	3.7 ^{ar}	3.5 ^{ar}	10.6 ^{cde r}	50.5 ^{br}	10.4 ^{dr}	11.0 ^{ar}
T94	Ctr	4.7 ^{cd s}	30.3 ^{br}	3.0 ^{br}	1.0 ^{cr}	1.1 ^{br}	9.0 ^{cd r}	51.0 ^{cr}	20.3 ^{ar}	5.8 ^{cr}
	Heat	9.7 ^{cr}	35.6 ^{ar}	3.0 ^{cr}	1.6 ^{cd r}	1.5 ^{cr}	9.8 ^{de r}	38.9 ^{cs}	17.9 ^{ar}	4.0 ^{br}

DBI=[(%monoenes + 2 x %dienes + 3 x %trienes) / %saturated FAs]

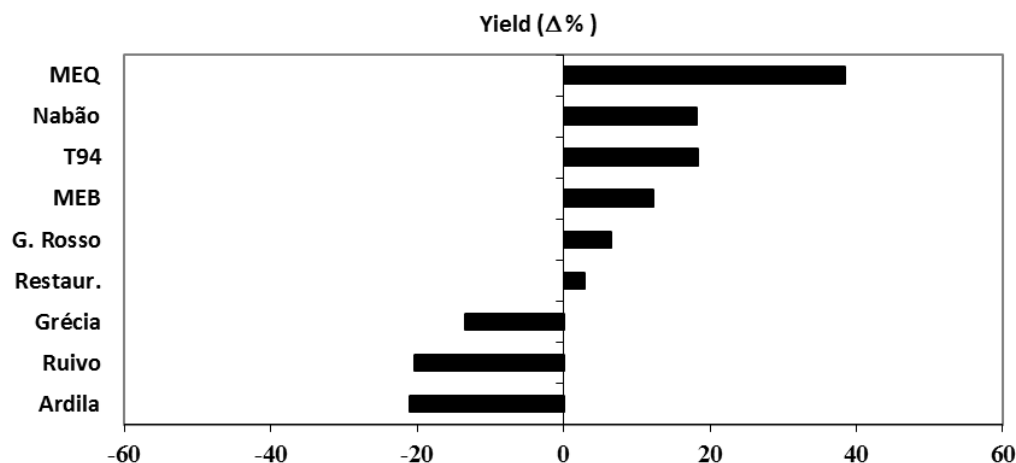


Figure 3. Changes induced by heat in grain yield of nine *T. aestivum* genotypes, expressed as percentage of variation of kernel yield (g plant^{-1}) in relation to control.

Discussion

The optimum temperature to achieve maximum yields of wheat is generally considered to be between 15 and 20°C during grain growth (Dupont and Altenbach, 2003). However, short periods (3-5 days) of high temperature ($\geq 35^\circ\text{C}$) occur quite often during the grain filling stage of wheat (Semenov and Halford, 2009), in the major Portuguese producing regions. It was reported that high temperature reduces the rate of transport of assimilates from vegetative organs to kernels, resulting in significant grain yield reductions, although high-temperature sensitivity differed amongst varieties (Plaut et al., 2004). Therefore, the present experimental conditions intended to study the high temperature impact in yield by simulating heat stress peaks that frequently occur in the field immediately after anthesis. Results concerning leaf gas exchanges denoted some variability in wheat responses to high temperature. Higher or stable P_n may occur, but the majority of genotypes depicted P_n decreases. It is conceivable that CO_2 gas-exchange is hindered at high temperatures by closing of the stomata (Matos et al., 1998).

Excessive heat increases transpiration and leaf water deficit may rapidly become so severe that stomata may close as a result of water-stress. In our case, the P_n decreases did not result from stomatal closure, since all genotypes showed higher or unaltered g_s values, accompanied by C_i increases, except in Restauração and Ruivo (which did not show P_n reductions). Therefore, when existing, the observed P_n drop would result from non-stomatal effects that hampers photosynthetic metabolism. As temperature increases, the CO_2 compensation point

may rise (especially with C_3 plants), resulting in an increase in intercellular CO_2 concentration (Bauer et al., 1975). Also, the decline in net photosynthesis at high temperature in C_3 -grasses is due to a strong increase in respiration (Matos et al., 1998).

Effectively the high temperature limit of net CO_2 uptake (maximum temperature for net photosynthesis or heat compensation point) is a resultant of two counteracting temperature-dependent processes. One involves the enzyme reactions of photosynthesis, the rates of which increases with rise in temperature in the lower and medium range, but are strongly inhibited by high temperatures. The other is respiration, which increases more rapidly than P_n with rising temperature (Bauer et al., 1975).

Considering sources for non-stomatal disturbances in P_n the impact on PSII activity might have contributed to P_n reductions in Gentil Rosso, Grécia and Nabão, as inferred from decreases of F_v'/F_m' and (ϕ_e) , observed in these genotypes. High temperatures could induce hyperfluidization of thylakoid membranes, affecting lipid-protein interactions and causing various disturbances, such as phase transitions of lipids and conformational changes (Raison et al., 1982). The transition from liquid crystalline to liquid phase of bulk thylakoid lipids causes changes in microenvironment of chlorophylls (Tovuu et al., 2013), that may alter photochemical efficiency of PSII. The remaining genotypes displayed quite stable values of F_v'/F_m' , (ϕ_e) and q_p , suggesting a lower thermal sensitivity of the photochemical apparatus of photosynthesis to heat (Matos et al., 2002).

On the other hand, photosynthetic activity was stimulated after heat exposure in MEB, whereas MEQ and Restauração displayed stable g_s and WUE enhancement, as well as greater kernel yield increases ($g\ plant^{-1}$) under heat, particularly in MEQ (38% increase). MEQ overcame P_n impairment (24% decrease) and Restauração slightly increased P_n (8%) and presented a concomitant and unique C_i reduction (26% decrease). In a former comparison of ancient bread wheat cultivars, the highest photosynthetic rates occurred in Restauração under heat stress (Scotti Campos et al., 2011a), what is in accordance with our present results which denote an enhancement of photosynthetic ability in these genotypes under high temperatures.

The maintenance of chlorophyll *a* fluorescence values in most of the genotypes further agrees with the impact on cell membranes. Differences in membrane selectivity and membrane injury have been widely used as an indicator of protoplasmic tolerance to abiotic stresses (Campos et al., 2003; Matos et al., 2009; Scotti-Campos et al., 2011a). Changes in membrane lipid composition may highlight plant mechanisms that help to avoid or to cope with membrane damage that would result in impaired cell metabolism (Campos et al., 2003; Partelli et al., 2011). Higher membrane stability (lower leakage) occurred in Ruivo and MEQ under heat. In the case of Ruivo, a higher protoplasmic tolerance as well as unaffected P_n may be related to the stimulation of membrane lipid biosynthesis, as inferred from higher TFA values under heat. This may correspond to a plant acclimatory response to assist membrane repair, eventually occurring under stress as reported for other species under environmental stressful conditions (Campos et al., 2003; Matos et al., 2009; Partelli et al., 2011; Scotti-Campos et al., 2011b; Medeira et al., 2012). In MEQ high membrane stability is in accordance with high lipid content (high TFA) and low unsaturation of membrane lipids (low DBI) in control plants, which were unaltered under heat. All genotypes showing high lipid amounts in control plants displayed raises in kernel yield, except Nabão. Previous studies showed that, under heat stress, genotypes MEQ and Ruivo displayed high P_n values while maintaining considerable yields, expressed as 1000-kernel weight (Scotti-Campos et al., 2011a). Present results further points that membrane lipid composition, as well as preservation of membrane integrity and stability, may also be involved in the maintenance of a better photosynthetic performance of several genotypes after exposure to high temperatures.

Conclusions

Results obtained in this work highlighted several responses among genotypes that can be related to a better performance under heat stress. Stable g_s and WUE enhancement in the cultivars MEQ and Restauração, increased P_n in the cultivars MEB and Restauração, or P_n stability in the cultivar Ruivo, denote an enhancement/maintenance of photosynthetic ability under high temperatures, in accordance with previous observations. Except for Nabão, more abundant lipids in control plants of cultivars MEQ, T94, MEB and Restauração corresponded to better kernel yield increases ($g\ plant^{-1}$) under heat. MEQ also presented the less unsaturated membrane lipids (low DBI) in control plants, which were unaltered under heat conditions. A stimulation of lipid biosynthesis was observed in Ruivo. Such traits related to membrane composition and stability in Ruivo and MEQ might explain their reduced membrane damage (lower leakage) under stress, suggesting a higher protoplasmic tolerance to heat.

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REGULAR ARTICLE

Pfeiffer wheat: An old variety with a bright future

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Abstract

Last century, the old winter wheat Pfeiffer was derived from a spelt by breeders in the biodynamic farming movement. The variety has practical significance because of reduced threshing problems. It has historic significance because it is the result of the exercise of an alternative perspective on breeding and heredity. The derivation of this wheat was the result of phenotypic selection of a feral spelt found in Italy in the time period between 1928 and 1940 by a team of breeders working in Germany, Holland and Switzerland. Plants were seeded at different times of the year to induce phenotypic changes; this was coupled with selection pressure for the bread wheat type of ear. Though all plants initially had typical spelt phenotypes (lax heads with brittle rachis and glume enclosed kernels) a few mutations, possessing compact heads and bread wheat heads, were found and selected on all sites and fixed for bread wheat head type on two of the three sites. Proposed explanations for the transformation (outcrossing to a bread wheat, mutation, atavism, or action of a living archetypal agent), are discussed in the light of the available evidence and heredity of domestication events for wheat and maize.

Key words: Wheat, Spelt, Epigenetic, Biodynamic, Domestication

Introduction

Over the last two decades I have had the opportunity to evaluate and select an old hexaploid bread wheat variety called the Pfeiffer wheat, that was derived from a spelt variety called Rome. I received the Pfeiffer wheat from Mac Mead of The Fellowship Community in Spring Valley, New York in 1994. They had obtained it from Erika Sabarth who had selected it in Spring Valley for decades under the direction of Ehrenfried Pfeiffer, a famous pioneer of biodynamic farming in North America. It was grown by Mac Mead for several years before I obtained it. The wheat had a long-term history of having been bred by biodynamic researchers in Europe. After receiving the wheat I grew it and selected it for adaptation to Midwestern conditions. It was grown for three years in conjunction with tests of wheat at Michael Fields Agricultural Institute. Afterwards it was grown independently by myself for multiple years and selected for winter hardiness, foliar disease resistance, and uniform, dark grain color. In one of

the early years of selections harsh winter conditions decimated up to 75% of the stand. The subsequent selections have demonstrated adequate winter hardiness for Wisconsin conditions.

The practical significance of this wheat is that it represents a free-threshing selection from spelt that may combine the nutritional value of spelt with an easy-to-harvest ear form. This is important because it could greatly decrease the costs associated with harvesting and processing spelt seed which is encased in glumes and needs to be milled out of its enclosure. Because pure spelt is a conceptual reality in the marketplace, it is important to know if the variety was derived from an outcross with wheat, or through mutation(s). But there is additional theoretical significance of this wheat in that those who bred it believed it to represent the result of an unusual trans-mutation event. The description they gave of this transformation does not easily fit with current modes of thinking about domestication events. The discrepancies with conventional genetic thinking were not resolved and were forgotten. And finally, the spelt project is one of the first breeding efforts of the biodynamic farming movement and probably helped shape their approach. In the following we will explore the interesting history of how this wheat was developed, discuss what it might be, and examine the biodynamic perspective on breeding in contrast to conventional approaches.

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The biodynamic movement and selection of primitive grasses

The Austrian philosopher Rudolf Steiner (1861-1925) developed a movement called Anthroposophy (Wisdom of Man) that was concerned with what he called a spiritual-scientific approach to life. In a course given in Germany in 1924, he outlined a form of organic farming which was subsequently called the biodynamic agricultural method (Steiner, 1993). Steiner was concerned with a general decline in food quality associated with the introduction of chemical-fertilizers. He indicated that chemical fertilization practices would produce large yields and produce products that were big and attractive in appearance. However, they were increasingly becoming 'stomach filler' with declining taste that did not properly foster human health and development. The decline in soil and crop health and nutritive value of crops (wheat, potatoes, barley, oats, alfalfa, etc.) paralleled the need for ever more new cultivars, a general increase in crop and animal disease, a growing fragility of agricultural systems, and a decline in human health and in the ability for humans to fully manifest their highest intentions in deeds. Steiner stated that by the end of the 20th Century common food products would have degenerated to the extent that they could no longer be useful for human nutrition. He suggested changes in attitudes towards farming, including the principle of forming the farm as a relatively closed, self-sustaining system with respect to manure and fertilizers, the integration of animals, the use of biological preparations as medicines for the earth and crops, and the forming of healthy farm-landscapes, as remedial measures.

He also suggested that his students apply these methods and try to domesticate primitive grasses in order to produce new cultivars for bread production with 'strong seed forces' (Pfeiffer, 1958). As a breeding measure he suggested alternating the planting dates of cereals closer to the summer or closer to the winter to engender beneficial changes in the plant's constitution. Biodynamic breeding efforts began and continue today with a range of domesticated crops.

Materials and Method

Probably the most useful results were obtained by selection from what appeared to be a semi-wild selection of spelt (*Triticum aestivum subsp. spelta*) obtained by another of Steiner's students by the name of Ehrenfried Pfeiffer from the Rome Botanical Garden in 1928 (Riese, 1940). The variety was mistakenly named 'Einkorn' (*Triticum*

monococcum L. subsp. *monococcum*) but was identified as a hexaploid spelt and renamed 'Rome.' Its plants had a facultative growth habit and could be grown both in spring and winter plantings. They produced a fragile rachis, and seed possessed typical spelt-type spikelets with hull enclosed seeds, and with few kernels in each spikelet (see photo 1). Over more than a decade offspring were grown out on several sites on a yearly basis, sometimes with alternating summer and winter or late summer and early winter planting dates. The plants were closely observed and selected for forms similar to bread wheat. The breeders selected for looser glumes, greater numbers of seed in spikelets, and a more stable rachis. Changes in head type in the direction of bread wheat occurred on all sites. The work was disrupted by the Second World War. No numerical analysis of the data is available.



Photo 1. Rome Spelt (taken in 1936).

Results

The overall work on the wheat from 1928 to 1940 in Dornach, Switzerland was reported on by Erika Riese (1940). They continuously planted out the most bread-wheat-like lines from the preceding year. Results with selection varied from year to year. Bread-wheat-like characteristics, such as seed-growing-through-glumes, or more grain/spikelet, manifested in the harvests of 1932, 1933, but in 1934 no changes from the spelt type were apparent. In 1938, ears with grain growing through glumes and condensed club-wheat like ears were harvested. In 1939, no changes from the normal spelt type were apparent. By 1940 continued selection resulted in a plant with ears that appeared to be a transitional state between spelt and wheat with broad, multi-grained spikelets, but the stability of this form remained to be confirmed by further grow-outs by the time of the final report available to us (Riese, 1940).

Voegele (1938) described his experience with the wheat in Pilgrimshain, Schlesien as follows:

“In 1931, I received glume-enclosed spelt seeds from E. Pfeiffer that possessed all the characteristics of spelt (*Triticum spelta*). These grains were derived from four generations of selection from a plant found in Italy which showed little similarity to a domesticated plant. The (*original*) ears and spikelets were unimpressive; the grains were formed but tiny and narrow. E. Pfeiffer began breeding the plant and after three generations derived a plant that was practically indistinguishable from white spelt. The rapid progress suggested that the predecessors of this variety had been cultivated, but the variety had become wild in its environment. In following years I planted this wheat in alternating seedings in either August or December. I obtained seed from these plantings that was identical to the parental plants. In 1934 in the plot that had been seeded in the previous December, a plant was found with five ears that had the appearance of a naked bread wheat (*Triticum vulgare*). I assumed that the plant was derived from a seed which had accidentally been introduced either through inattention or by an animal, and I was prepared to rogue it out. However, the fact that the form of the ear did not resemble any of our local wheat varieties kept me from doing so. Closer observation revealed that the ear was a transitional form between spelt and bread wheat. A strong rachis, holding the spikelets together, was apparent though it was not as strongly expressed or strong as in common bread wheat. The appearance of the glumes resembled spelt. After

that discovery the plant was of course allowed to ripen. I harvested it myself. When rubbing the seeds out, the transitional characteristics became apparent. On the one hand the rachis was not totally established; on the other hand it was difficult to rub the fully ripe and hard grains from the glumes. The elongated kernels resembled spelt.

At the end of September and again at the end of December, two different beds were planted with the offspring of this plant. All the plants emerged. The September seeding tillered strongly before the beginning of winter. The December seeding emerged in February but shortly afterwards was severely damaged by pheasants so that only 13 plants remained. All these plants grew to ripeness. As long as the ears were not visible there was no particular difference between individual plants. I expected that the daughter plants were the same as the parent and the transitional form would manifest again. This expectation was not confirmed. As the ears shot up in July of 1935, the unexpected impression was that every plant had a different type of ear. Any observer that did not know the previous history of the planting would have had to conclude that a mixture of the most different spelt and wheat varieties had been seeded there.

On the one hand, very different ear forms appeared. Next to plants with extremely long and loosely set spikelets on spelt ears with long straw were short, uncommonly compact ears on short straw, which resembled *Triticum compactum*; between these cylindrical ears of all kinds appeared. A greater diversity of form would not have been achieved if each of the planted seeds had derived from a different spelt or wheat variety. Because I harvested the seed from the mother plant myself, had rubbed them from their glumes myself, had kept them under lock up to planting, and then had seeded them myself, it could not be doubted that the resulting plants that produced the chaos of forms were derived from the mother plant.”

I was unable to find a description of the selection history at the Loverendale experimental Farm in Domburg, Holland including methods used or dates of its inception and end. Seed was sent to Martha Kuenzel in Loverendale for selection after being grown in Dornach, (Mos and Heyden, 2006, Schmitt, 2006). Photos exist in the Pfeiffer Archive of the 1934 harvest of the first larger scale planting of the spelt on a very small field, which filled a wagon with bundles, so it could be conjectured that the variety had been under selection and multiplication since at least the fall of 1931. A transitional, spelt/wheat form was found in 1935

and became the basis for fruitful breeding in Switzerland and later in the USA. Seed of 15 breeding lines from this program were apparently given to Dornach for further breeding in 1937, renamed 'Dornach Rome', and planted in September 1937 and subsequent years. Another set of 6 elite lines were obtained by Riese from Holland in 1939 and planted in Switzerland in October, 1940 (Riese, 1940). Photographs of elite lines from Loverendale 1935, 1937, and 1938 were found in the Pfeiffer archive. The transitional form found in 1935 in Holland was described by Riese (1940) as follows:

"In 1935 a spelt plant with a very promising appearance appeared at Loverendale with very solid, beautifully formed, multi-grained spikelets (see photo 2). The seeds of these ears were grown out and all kinds of wheat types and transitional forms appeared in the course of several years (see photos 3-7). This included: pure spelt types with closed spikelets, spelt types with open spikelets, closed spelt types with bread wheat type kernels, condensed club wheat types, in part with empty undeveloped spikelets, and elongated, threshing capable forms with strong rachis and spelt type kernels as well as with bread wheat type kernels. We called the latter ear form 'Theodora.' From the photographic series made available from the Pfeiffer archives it seemed apparent that Theodora had been subsequently re-named 'Reward'.



Photo 2. Loverendale transitional mother plant (1935).

Riese suggested that the cause of the mutation was due to shifting climate and soil types. She described the stages of the manifestation of the mutation as follows:

"First stage: On an especially beautiful ear that is well formed from base to tip, one finds the beginnings of a stabile rachis and looser glumes. The grains appear refined and there are three or four grains in each spikelet. **Second stage:** From the offspring of these grains plants appear that have condensed club ears. They can be two rowed but despite that look tousled and angular. The highest and lowest spikelets on these ears are too densely jammed together and are empty of seed. The straw is short; the grains are shriveled, often too light and look like spelt seed. **Third stage:** The ears stretch out again and become longer, with strong rachis and open glumes (the second stage had half open glumes, a partly strong rachis, and are less pleasant to thresh out than totally encased spelt spikelets). They often have empty tip spikelets or fragile parts; there are sometimes spelt-like and sometime wheat-like kernels in such ears. **Fourth and last stage:** An open ear develops with a strong rachis that is threshable. Most of the grain looks like wheat grains; that means smaller, more compact, rounder, flatter in the crease and especially vitreous.

It seems to me that the changes in Rome generally followed these stages but numerous transitional forms could be found. The special characteristic of these plants is that three kinds of forms, that is spelt, cylindrical, and the Theodora type of ears could appear on one and the same plant. In Holland and so far as I know in Pilgrimshain, these transmutations occurred in 1935 and 1936. In Dornach something similar finally appeared in 1939/1940. That needs to be confirmed by results in 1941.

Our spelt mutation was a unique origin and development. Though it was derived in a short period of time, in most cases it did not appear suddenly, but rather the changes occurred gradually, through several growing years, on a single plant often with different transitional stages. The same plant could have both normal and varying ears on its straw.

Privy councilor Bier (1934) observed analogous processes when breeding lupins also under biodynamic conditions and characterized them under the name 'transmutations'. By transmutations are meant changes that suddenly appear within a growth period but at least in part show transitional, or in-between forms, so that the complete, natural working through of the forms can take place over several growing seasons. These

forms are constant in their inheritance, without segregating after Mendelian laws, but they find shape mainly in the course of a few years.



Photo 3. Wheat type 4, Dornach, 1937.

Definite, parallel changes in single plants, so called correlations could be established. Many of these are known from normal cereal breeding with crosses. The most significant were: 1) stronger formation of straw paralleled less tillering. Relatively strong tillering can naturally be achieved by cultural measures such as transplanting and cultivation, but that has nothing to do with inherited characteristics. 2) An ear became multi-kernelled, open in its glumes and strong in rachis, though the full formation of these traits by our 'transmutation' took place over multiple generations. 3) If a condensed, cylindrical ear developed, the straw was also shortened by a shortening of internodes and more strongly formed. There was no correlation between the form of the grain and of the ear. In typical spelt ears with fixed, closed spikelets, it is

possible to occasionally find bread-wheat-like kernels. In typical wheat ears it is possible to find both wheat and spelt-like kernels and transitional forms. It remains to be seen whether or how those forms will change in the future."

Katherine Castelliz (1989) who participated in the project wrote: "When I came on the scene in 1938 there was a variety of different ears, sometimes even on the same plant...Among the variety of forms developed were some stable ones. There was one particularly beautiful one which Ehrenfried Pfeiffer took with him to America. The ear was three to four inches long, had a firm axis and 4-5 grains per spikelet. However, the grains were of the common wheat type whereas the original plant, as well as some of the later derivatives had typical spelt wheat grains. The shape of either of them is very distinct. The grain was readily threshable."



Photo 4. Wheat type 3, Dornach, 1937.



Photo 5. Wheat type 7, Dornach, 1937.

Discussion

Why did the transformation happen? These results can stimulate questions of how the transformation was elicited and what was its basis? Voegelé (1938) suggested four different possibilities.

- 1) The transformation was due to the activity of a creative inner principle or archetype that lives in wheat and is capable of breaking hereditary barriers and transforming one form of the species into another.
- 2) The transformation was due to contamination, especially due to outcrossing of spelt with bread wheat.
- 3) The transmutation was due to a genetic mutation.
- 4) Transformation was due to a throwback to an atavistic form.

There could be various combinations of overlapping truth in explanations between explanation 1, 3, and 4, but it seems as if explanation 2 is true all other proposed

explanations may be false, so we will explore it first.

Outcross

It would be easy to quickly dismiss the results as the result of an outcross. Crosses between European spelt and bread wheat often exhibit a range of ear types including lax spelt type and *compactum* types (Dvorak et al., 2012).



Photo 6. Wheat form 2, 1938.

Though possible, there are several arguments why this explanation is improbable for fitting all of the phenomena. Riese (1940) refers to the gradual, phasic nature of the changes, and also to observing different kinds of heads (spelt, cylindrical, and bread wheat type) on the same plants. As plants were individually transplanted it should have been possible to observe this. She also refers to a lack of Mendelian segregation with the transformation, suggesting that the evolution of form proceeded in a direction without segregation of individual traits.

The transitional forms noted in 1933 in Germany and in 1935 in Holland are similar to descriptions of spelt x bread wheat F1 plants

(Muramatsu, 1963). The variation of many types of ears described in Germany and Holland show a pattern reminiscent of that expected with a segregating F2 population. Voegelé (1938) mention that the forms that appeared in 1934 in his garden had maintained stability for more than four subsequent generations, but that does not mean there was no variation within the forms. Riese (1940) stated that after having received the 15 Lowerendale selections in Switzerland in 1937 she categorized them into 16 types according to their ear type, with one type being a mixture of all forms, but grew only 14 types again in 1937. Photographs 3-7 show ear forms within the different selections from 1937 and 1938. In 1939 she discarded some lines because: "Different types were discarded because they were not pure or not healthy, too unstable, or poor ripening." She only grew 12 types in 1939. Also after having received the second set of (6) breeding lines from Loverendale in 1939, she states that several of them were discarded as being backsliding spelt types.

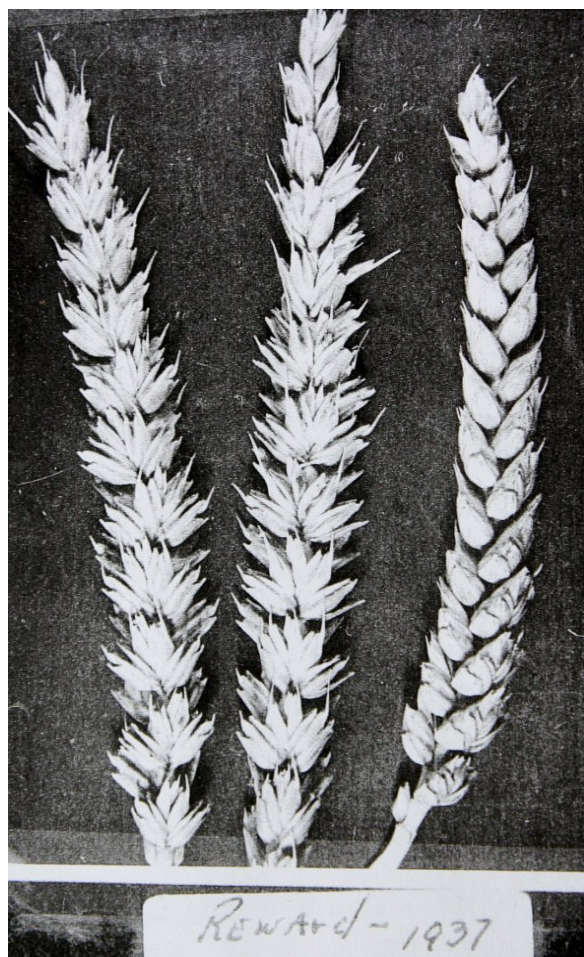


Photo 7. Theodora/Reward ear types, Dornach, 1937.

Boshnakian (1922 and 1923) studied crosses between spelt and bread wheat and linkage between rachis strength and glume tenacity. He also found strong dominance of the spelt ear type in the F2 followed by segregation in the F3 generation for ear density, probably associated with segregation of forms of the C gene. Neither of these segregation patterns were reported by Riese (1940) or Voegelé (1938).

If outcrosses occurred, then when, where, and how often? Descriptions and photographs of the Swiss breeding program suggest that protocol involved plants seeded in the fall being transplanted out into the field in the spring into isolated bird and animal proof cages, possibly to obviate contamination as well as to reduced depredation. Bread wheat was not part of their other plantings. Yet they recorded seeing compactum type heads and soft-glumed phenotypes with variable stability in their evolving set of spelt lines which only gradually became bread-wheat like. Though there were some ears noted already in 1930 with grain growing through glumes, club wheat ear types, combined with weak glumes, appeared first in 1937.

Meanwhile the breeding programs in Germany and Holland had been separate from the Swiss program and operational for several years before transitional forms were observed on each site in 1933 in Germany and 1935 in Holland. If outcrosses are to explain results in Switzerland, Holland and Germany, they would have had to have been separate outcrossing events, taking part in different years.

We do not know if bread wheat was planted near to the spelt plantings in Holland or Germany. But a review of recent field research on outcrossing in wheat (Anon. 2006a) suggests that outcrossing is generally a very seldom event; only up to 1% if plants are spaced approximately 30 cm apart and minimal or non-existent after that. Voegelé (1938) argued that spontaneous European spelt x wheat crosses are either rare or non-existent. Furthermore, on the basis of the appearance of offspring, Voegelé (1938) denied that other wheat cultivars existed in his region that resembled the offspring found in the spelt plantings.

The possibility of outcross, though probably implausible for explaining all the results, cannot be ruled out without further investigation, such as marker selection work on storage proteins in grains. Though there is no source of the original spelt seed to use as a check, other European spelt cultivars

might serve that purpose to test the Pfeiffer wheat that is available today.

Mutation

Several genes are thought to play a role in controlling the stability of the rachis, glume structure and openness in hexaploid wheat. The brittle rachis loci (*Br1*, *Br2*, and *Br3* located on the chromosomes 3D, 3A, and 3B, respectively) have recessive alleles that reduce brittleness. *Tg* (tough glume) located on the short arm of chromosome 2 affects the morphology and hardness of glumes and a recessive allele *tg* conditions soft glumes that allow for free threshing. The *Q* gene, located on the group five chromosome of the AA genome is pleiotropic for domestication traits; it reduces rachis brittleness, loosens glumes, and induces compact, 'square headed', and free-threshing ears (Fans et al., 2013; Simons et al., 2006). The *Q* allele is a hypermorph or more active form of the *q* allele in conveying effects of domestication (Muramatsu, 1963). It differs from *q* by only one amino acid sequence. The *Tg* allele is epistatic to the *Q* allele, inhibiting its action (Fans et al, 2013; Simons et al, 2006). Though *Q* is often cited as a super domestication gene its action is strongly modified by the background it is in. The less active *q* gene is found in European spelt (Luo et al, 2000). When placed in a domesticated wheat background *q* produces a more 'speltoid' ear but does not result in a fully hulled ear and the rachis is not brittle (see figure 1 in Luo et al, 2000). The background heredity of spelt conveys additional primitive characteristics to the ear (Muramatsu, 1963).

If changes in the German and Dutch spelt were due to a single mutation, it must have been a change from *q* to *Q*. However, the *q* gene is thought to have originated only once (Simons et al., 2006). The simple mutation explanation has similar problems for fitting the described phenomena to the outcross explanation. Again, Riese (1940) described gradual, phasic changes, and also observed different kinds of heads (spelt, cylindrical, and bread wheat type) on the same plants. As plants were individually transplanted it should have been possible to observe this. To explain the changes as a single mutation it would be necessary to assume a very variable degree of penetrance of the relevant mutation in individual plants. Voegelé (1938) does not describe phasic changes past the second generation on the bread-wheat-like derivatives. Forms remained stable for four generations after the change occurred; this lack of segregation does not fit a Mendelian explanation of a simple mutation either.

Throw-backs or atavistic changes

Mutations occasionally occur in normal bread wheat changing square headed ears into so called lax speltoid (= spelt like) ears. These mutations are often very unstable and mostly revert to compact ears called 'subcompactoids' (Sanchez-Monges and Mac Key, 1948).

Voegelé (1938) was aware of the spontaneous mutation of wheat to speltoids; in his time this was characterized as a throw-back to atavistic forms. The common theory in his time was that wheat had evolved from spelt (McFadden and Sears, 1948). From Voegelé's perspective it was difficult to look at the transformation of spelt he had experienced as a throw-back; rather he saw it as a repetition of the evolution that had occurred to develop wheat out of spelt.

However, it turns out the evolution of European spelt is different than was previously thought. The current theory, supported by molecular data, is that one of the original parents of spelt was a hulled, tetraploid emmer (*Triticum turgidum* subsp. *dicoccon*) and that the other was free-threshing, bread wheat. Thus wheat did not evolve from spelt, spelt evolved from wheat. This theory is in consonance with archeological findings (Dvorak et al., 2012). It is supported by the fact that most European spelts have an active *Tg* gene in the B genome and an inactive *tg* gene in the D genome (Dvorak et al., 2012). Furthermore, evidence from investigation of the high and low molecular weight glutenins suggests strongly that the free-threshing bread wheat ancestral to European spelts was most probably *Triticum aestivum* subsp. *compactum* or club wheat (Yan et al., 2003). This explains the fact that when European spelt is crossed with bread wheat, the F2 generation mostly segregates out spelt, square-head, and compact ears and why activity at the C gene locus, conditioning compact ears, is present in spelt (Dvorak et al., 2012).

Thus changes observed by the Riese and Voegelé studies (spontaneous shifts to club wheat ears and free threshing structures) could actually be due to a throwback to the parents of European spelt which included club wheat. If so, the main activity of the spelt researchers might have been inducing the shift and stabilizing it. The results of the Swiss researchers suggest that the transformation was latent. The more aggressive alternating planting methods practiced by Voegelé (September and end of December, seed emerging in the spring) might have triggered phasic shifts leading to mutations, changes in epigenetic regulation, or reversions to atavistic patterns (in this case free threshing, compact ears, etc.).

Atavisms, mutations, domestication, and induction of atavistic patterns

In consideration of atavisms as a possible explanation for the results it is useful to discuss domestication phenomena associated with phenotypes of maize. Iltis (1983 and 2006) characterized ear-tassels in maize as a very common atavism, induced in part by environmental factors. Ear tassels are transitional forms between tassel and cob; they are prevalent on primitive maize cultivars and not on modern cultivars. The ear-tassel atavism is a relic of maize's domestication history and particularly the creation of the ear, and it is selected against in corn breeding programs. Iltis described the formation of the ear as a condensation of an axial, primary branch of teosinte, with leaves on the branch becoming husks and tassel flowers changing sexuality from male to female thereby producing naked seed. He described this phenomenon as a 'catastrophic sexual transmutation.' In maize, ear tassels occur not on axial branches, but rather on basal tillers. Convincing information relating domestication to changes in single genes was not available at the time of his initial publication and he related the transmutation to changes in environmental factors inducing shifts that were then subsequently stabilized by human selection.

Since then, a great deal has been discovered (especially by the work of the lab of John Doebley at the University of Wisconsin) about allelic diversity in genes that anchor the differences in floral and fruiting structures between teosinte and maize. The maize allele of the teosinte branched1 gene (*Tb1*) causes stronger apical dominance, inhibits the formation of axial branches, and causes a feminization of tips of branches (ears and ear tassels on tillers) (Doebley et al, 1997; Hubbard et al., 2002). In addition to this, the maize allele of the teosinte glume architecture gene (*Tga1*) induces a loosening of the glume, exposing the seed from its cupulate shell (Dortweiler et al., 1993).

It is interesting that the word '*transmutation*' was used by Voegelé (1938) and Riese (1940) working with spelt, and by Iltis (1983) working with maize for the transformation to domesticated floral structures that transcended static patterns associated with individual genes (trans-mutation). There are common elements associated with domestication of both wheat and maize such as reduced losses of seed and easier harvest, easier access to naked seed, loss of a hulled seed condition, enhanced condensation and re-

arrangement of floral parts, and strengthening of a rachis structure.

Noteworthy are the two opposite directions of the transformations of broadhead and spelt ear types into each other. These are: broad-headed, non-club, bread wheats transforming to lax speltoid and then mostly reverting to 'subcompactoids' (Sanchez-Monges and Mac Key, 1948). Or the gradual progression noted by Riese in Switzerland of lax spelts transforming to compact and then to broad-headed types.

Searching for atavistic patterns may indicate but not necessarily explain domestication events. However, the induction of atavistic growth patterns may be associated with environmental disruptions, and this may explain some of the results achieved in the spelt conversion as mentioned above. This author has noted other atavistic phenomena in his corn breeding, but only following planting under climatic conditions that are non-endemic to the variety and therefore disruptive to plant morphogenetic processes.

The first was the appearance of teosintoid-like axial branches along the main axis of corn stalks when the Peruvian corn races Piricinco (Amazon) and Mochero (Northern Coast) were grown under modified temperate daylight rhythms in Wisconsin in 2009, and also when crosses of adapted cultivars with Mochero were grown in Wisconsin in subsequent years. Botanical descriptions of growth patterns of Piricinco and Mochero landraces in Peru (Grobman et al., 1961) are of early flowering cultivars which only rarely express tillering, and no indication of axial branching at all. The phenomena observed in Wisconsin are strongly reminiscent of the action of the teosinte *tb1* allele on maize (Doebley et al, 1997).

The second atavism is associated with growing Wisconsin corn under tropical daylength conditions. In particular, corn from the Mandaamin Institute breeding program (S2 inbred derivatives between a cross of two populations (LH119 x LH132 and AR16021 x B73) bred in Wisconsin were grown in a winter nursery in Puerto Rico in 2011/2012. Tassels appeared in ear shoots and as well as primitive grassy tillers in some corn plants that were mostly normal in appearance. These growth patterns are similar to the action associated with the teosinte *tb1* allele (Doebley et al., 1997). In 2012, when the next generation of those corn breeding lines was grown in Wisconsin, one of the S3 breeding lines segregated out both normal and what appeared to be pure grassy-tillered phenotypes, with very narrow leaves. The lines

appeared otherwise to be short, otherwise uniform, and inbred so we assumed no recent outcrossing had occurred.

We are not and have not been breeding with teosinte, so these results are probably not due to outcrosses with teosinte, but rather to internal factors and tensions associated with environmental signals.

Transforming activity of a creative plant archetype; a Biodynamic perspective

It is important to clarify what Voegelé (1938) meant with this explanation in which he refers to Goethe's botanical studies and Steiner's interpretation of them (Steiner, 1950). Implicit in Voegelé's exposition is the concept that an inner, essential living principle, evolving archetype or entelechy lives in and encompasses related species and can transform barriers between them. This type lives in the expansion and contraction of growth and forms in the plant and is inwardly perceptible to a schooled power of perceiving and thinking in the sense of Goethe's 'anschauende Urteilskraft' (literally translated as beholding power of judgment) (Steiner, 1950).

Regarding the transformative activity of the archetype, Voegelé refers to the results of August Bier (1934) who observed transformation of phenotypes of lupin species after growing seed which had been dormant for a half century in the soil.

Voegelé (1938), and other biodynamic researchers accepted that genes and chromosomes were structures by which the archetype achieves stability and expression in different forms and species (Pfeiffer, 1958, Engquist, 1970). However genes were not viewed as the source of evolutionary changes. Voegelé cites Bier (1934) regarding explanations based purely on genetic mutations as follows:

"Let us assume such a chromosome mutation was found. This would not really explain anything. The question as to why plants change would simply have become the question as to why do chromosomes change."

Furthermore, Voegelé states: "In the light of extensive knowledge gained in genetics it may be assumed that the mutations described above followed changes in the seeds' chromosomes or genes. But anyone wanting to see such chromosome changes as determining the transformation that follows would only have gone half the distance in his thinking. If I know from earlier observations for example, that ruts going in a particular direction were made by a cart, I cannot

stop at the horse and the cart looking for the factor responsible for those ruts. It should be evident to everyone that I have to go on to the driver who put the horses before that cart and decided which way it should go. Yes, the cart and horses pulling it produced those ruts, but the determining factor was the drivers will."

Voegelé's biodynamic perspective is not opposed to genetic research but rather broadens the perspective of the role of genes in the unfolding of crops and considers them in the context of the active principle working to form the whole plant. Voegelé's perspective is also in consonance with the recent mission statement of the Association of Biodynamic Plant Breeders (Anon. 2006b) which implies recognition and appreciation of the inner principle/archetype active in the crop plant of choice, and perhaps even re-conceiving the work as being a kind of partnership. It seems obvious that the performance of the inner archetype has been conceived of as being the provenance of practical breeding. Whether the plant archetype that lives in the species brings itself to optimal expression within the genetic framework and environment that the breeder has a hand in creating should reveal itself in measurable form, yield and quality characteristics.

Voegelé's perspective on some kind of whole plant dominance over genes may not be empirically foreign to experience gained in practical breeding. In fact, it is a commonly recognized phenomena that whole plant performance often suffers with the introduction of novel single mutations that are introgressed with the intentions to improve a crop. Furthermore, developing 'perceptive judgement' is probably not a foreign concept or capacity to breeding as it was conceived of in the last century. Training the 'breeders eye' or 'gaining a sense of the organism' was a valuable opportunity and the result of constant learning built on observation and spending a lot of time with the species of choice. Of course, such human capacities are inadvertently 'selected against' by modern breeding approaches that confine breeder activity to farm machinery or labs and limit conceptual activities to genetic mechanisms.

Our predominant civilization presently views plants as genetic machinery whose evolution was determined by random generation of mutations pruned down by natural selection. The concept of an inner principle or archetype living in formation, utilizing, and evolving such structures may be heretical or anathematic for many. The conception of crop varieties as 'a technology that yields' (roadside advertisement in the U.S.A. for Pioneer

Hi Bred seed products in 2009), and use of genetic engineering to change organisms by rearranging genes from different species, is the natural outcome of the concept of the reductionist world view. However, this perspective is repugnant to many who sense there is more to an organism than a set of mechanically interacting genes, and view genetic engineering of food as a dangerous perversion.

Though Voegelé's dynamic explanation based on Goethe's findings offers us an alternative vision of plants and their evolution, and it fits many of the phenomena presented, his explanation is probably not conclusive to the wider scientific community based on the evidence that was presented. There are too many open questions that are difficult to answer due to lack of sufficient evidence of the simple facts of the case. In particular: What kind of variation existed after the transformations were achieved? Why were there differences in results between sites? Were the changes associated with outcrosses, mutations or epigenetic shifts or some kind of combination? Did the 'trans-mutational' changes referred to result in the production of stable mutations in chromosomes in the direction of domestication? Were they monogenic, multigenic, or changes in background effects? Were the phenomena a step forward or re-creation of ancestral forms?

Furthermore, as Goethe himself found (Steiner, 1950) it can be difficult to convince people about results of experience/thinking-based perceptive judgment if they are closed from the beginning to the possibility that such capacities can exist.

Conclusion

Clearly the explanations available to us up to now do not bring us to unequivocal decisions as to what happened to the spelt. All-in-all, better documentation of such 'trans-mutational' phenomena are critical before they would be widely accepted. The molecular tools needed for measuring changes in alleles and chromatin exist, but it is a question whether interest and readily accessible phenomena are available.

However it happened, the team of biodynamic breeders succeeded in creating a new wheat variety. Voegelé (1938) states that: "Irrespective of whatever theory we have, the fact exists that Nature, through a generous gesture, succeeded in creating a series of different bread wheat forms from spelt."

The Pfeiffer wheat, descended from the Lowerendale selections of Maria Kuenzel that was discovered 78 years ago, selected by Maria Kuenzel, Erika Riese, Erika Sabarth and myself,

sequentially named Einkorn, Rome, Theodora, Reward, and Pfeiffer, still exists (Photo 7, Photo 8) and may be made available to collaborators for appropriate genetic studies to understand its origin.



Photo 8. Harvesting Pfeiffer wheat in Delavan, Wisconsin, USA, 2012.

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REGULAR ARTICLE

The ancient wheats of Georgia and their traditional use in the southern part of the country

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Abstract

Georgia represents a biodiversity hotspot for wheat with high levels of endemism. Many local variations of wheat are found in the country due to its variable climatic, edaphic, socio-economic and cultural landscape. Local variations of seven free-threshing and seven hulled wheat landraces and old varieties are found in the country, along with wheat utilization and the different traditional uses, are described in this paper. Despite the diversity and significance of Georgian wheats, their role in the wheat phylogenesis has not been thoroughly studied and the general public is not well informed on the subject. This article aims to promote Georgian wheat landraces and underline the necessity of carrying out a detailed systematic inventory of the wild and cultivated plants in Georgia in order to get more information on the state of this national heritage and of the measures to be taken for its conservation.

Key words: Ancient wheat, Traditional use, Georgia, South Caucasus, Samtskhe-Javakheti, Ethnography

Introduction

Georgia is one of the centres of the origin of wheat within the Near-East centre of origin of cultivated plants. Out of about 20 wheat species known in the world in the earlier times, 14 were cultivated in Georgia, five of them are Georgian endemics. Many names of wheat can be found in the Georgian vocabulary. There is hardly another language in the world where the wheat has so many common or wheat variety names. The most ancient Georgian names of wheat found in the written sources are those mentioned in the oldest Georgian translations of the Bible ('Asli', 'Dika', and 'Ipkli'). In the later written sources, other names appear such as Zanduri (includes *T. monococcum*, *T. timopheevii*, and *T. Zhukovskyi*), Makha (*T. macha*, *T. Paleocolchicum*), Asli, (*T. Dicoccum*), Ipkli, (*T. aestivum*, bearded forms), Khulugo, (*T. aestivum*, beardless forms), Dika, (*T. Carthlicum*), and Tavtukhi, (includes *T. durum*, *T. turgidum*, and *T. Polonicum*).

The soft wheat variety name that is firstly mentioned in Georgian literature is 'Ipkli'; which is a winter bearded soft wheat species. Later the name begins to incorporate a large group of wheats being named as 'Dolispurebi' (Doli breads). These are: 'Tetri Dolispuri', 'Tsiteli Dolispuri', 'Shinduri Dolispuri', 'Tianuri Dolispuri', 'Korbouli Dolispuri', 'Meskhuri Dolispuri', 'Kheldeshuri Tsiteli Dolispuri', or 'Matsrani.' All these wheats are bearded forms. There are also introduced species such as 'Tetri Upkho' (White Beardless), 'Tsiuteli Upkho' (Red Beardless), 'Khulugo'. In addition to the above mentioned species, many landraces are known such as 'Adgilobrivi Khorbali' (Local Wheat), 'Semodgomis Khorbali' (Winter Wheat), 'Poshola', 'Khotora', 'Rachula', 'Gomborula', 'Gelatura', 'Dzalisura', 'Khozo', 'Dzveli Puri', 'Khuzala', 'Niksavra', 'Tskhratavtava', 'Tsiteli Parna', 'Paseni', 'Makhnia', and 'Topbashi'. This list of wheat names may contain synonyms, but, in spite of this, it was noticed that people in every locality tried to give the landrace cultivated in their locality a proper name that would be connected with the specific properties of the landrace. The second group of names belongs to the second by its economic importance wheat, the so-called hard/durum, or macaroni wheat *T. durum*. This wheat is relatively new as compared with soft wheat. In spite of this, it has many Georgian names.

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The common name, for example, is ‘Tavtukhi’, the spike of which can be white, black, red, gray, honey, ebony, and finally black-bearded in colour. From free-threshing wheat, of importance is Dika wheat. According to spike colour, there are white, red, black Dika wheats. Javakhuri Dika and Dika Ipkli are mixtures of soft and durum wheat.

Of the free-threshing wheat species, the following are also mentioned in Georgian chronicles, including the so-called ‘Chagvera’ wheat, which in some localities is known as “Kondara” (club) wheat - *T. compactum* Host, then the Polish wheat - *T. polonicum* L. and the English wheat - *T. turgidum* L. However, their distribution and economic importance was so insignificant that their local names are not known, although known is the local name of a branched-ear variety of the English wheat – ‘Kakhuri Datotvili’, developed by selection; however, it was rather unpopular and quickly fell out of favour and is not cultivated any longer. Another species - *T. turanicum* Jakubz., was found in Georgia. In 1923, in the Kartli village of Odzisi, P. Zhukovskiy described a new variety of this wheat - var. *odsissianum* Zhuk. No other evidence of the distribution of this wheat in Georgia is available. This variety is rather well distributed in neighbouring Azerbaijan, supposedly being introduced together with durum wheat species, which are very diverse in Azerbaijan. Thus, both hulled (seven species) and free-threshing (seven species) wheat were rather well distributed in Georgia. These species comprised in turn many local cultivars and landraces. Their exact number can hardly be established, particularly today when they are critically endangered by genetic erosion except for the germplasm material being preserved at several gene banks.

Main wheat species cultivated in Georgia

Free-threshing wheat Species

According to modern genetic classification, 7 out of 8 free-threshing wheat species were distributed in Georgia. One of them, *T. carthlicum*, is the Georgian endemic variety. These species were represented by numerous botanical varieties and landraces. The seven species are:

Triticum aestivum L., soft wheat, (common wheat, Ipkli, Khulugo, Doli, Photo 1): The oldest Georgian name of the species is ‘Ipkli’, this being evidenced in the first written sources (5th century AD). Later, only one landrace has preserved this name. The remains of soft wheat together with other cereals are found in the archaeological materials of the Neolithic Age in West Georgia and of the Eneolithic Age in East Georgia. Since then,

the soft wheat has spread in every locality of Georgia, which had at least minimal environmental conditions for wheat cultivation. This was possible due to the large diversity of the species including a large number of botanical forms. The diverse ecological conditions of Georgia made it possible to develop several ecotypes within one variant such as *T. aestivum* var. *ferrugineum*, the following three local varieties are known: Meskhuri Tsiteli Doli, Kakhuri Tsiteli Doli, and Svanuri Tsiteli Doli, which developed under completely different ecological conditions. The Meskhuri Dolispuri was developed under harsh climatic conditions to which it is adapted. The Kakhuri Dolispuri is adapted to almost subtropical conditions, whereas the Svanuri – to high-mountain conditions. Good taste and sustenance are the common traits of these landraces. The soft wheat species (*T. aestivum*) is also noted for its diverse biological properties - there are winter, spring and facultative varieties. The species of this wheat adapt well to heavy, poor soils, develop well under both irrigated and rainfed conditions. The grain size of the wheat cultivated under irrigated conditions exceeds that of the one grown under rainfed conditions, but is inferior to the latter in sustenance, fragrance and bread-baking properties. Therefore, this wheat was generally cultivated on rainfed land. Georgian species and landraces are also noted for their prolific tillering capacity, yield stability, resistance to shattering and some diseases.



Photo 1. *Triticum aestivum* L., soft wheat, (common wheat, Ipkli, Khulugo, Doli).

Georgian Doli wheat species are also noted for other advantages. However, these varieties have certain disadvantages as well. These landraces are prone to lodging under high input agriculture and

irrigation conditions, rust diseases, and small-grain size. In spite of this, the people have given it a pet name “Mother Wheat” and the bread baked from its flour – “Mother’s Bread”. Georgian soft wheat varieties are used to derive modern wheat species (Naskidashvili, 1978). Regrettably, these wheat species are critically endangered in Georgia. Fortunately, they are known and conserved in genebanks abroad. Thus, for example, Georgian Red Doli is sown in southern France which is known there as ‘Caucasus Rouge’.

Triticum carthlicum Nevski (Dika, Photo 2): According to its distribution and significance, the Georgian endemic wheat species Dika ranks second in Georgian agriculture. Dika is known as a spring wheat of the middle and high-mountain area, and since Georgia is a mountainous country and its population had to live at the altitude of 2000 m a.s.l. and over, a quality grain crop was to be cultivated. The wheat crop best suited this purpose. Dika fields were found at the altitude of 750-2000 m asl., however the main sowings were still located within 1000-2000m asl. At the altitudes over 2000m asl. Dika was represented as a cenosis - *T. carthlicum*, *T. aestivum* rather than independently. An example of the above is Javakhetian Dika – a combination of Red Dika and the spring soft wheat. Dika is characterized of a great diversity of forms. It is comprised of (1) mountain forest zone and (2) mountain steppe ecotypes; the first ecotype was distributed within the Great Caucasus Range forest belt (900-1400 m asl.), where the black-eared variety *fuliginosum* Zhuk. prevailed. It is grown exclusively in East Georgian mountain region Pshavi. It also makes the principal background in the sowings of Trialeti, Manglisi, and Marneuli (Bregadze, 1980). As a mixed crop, it is met within the Great Caucasus’s Enguri, Kvirila and Patara Liakhvi river valleys. In the second ecotype population, prevails a more drought-resistant, short-vegetation red wheat variety *rubiginosum* Zhuk.

This wheat is the main crop in the regions and districts of Samtskhe-Javakheti, Bakuriani, Borjomi Tsalka, Trialeti, Kartli, Pshav-Khevsureti, Mtiuleti, Tusheti, Imereti, Racha-Lechkhumi, and Svaneti. The white-kernelled variety of Dika - *stramineum* Zhuk., is found as a mixture in Trialeti, within the Rioni, Liakhvi, Enguri, and Kvirila river valleys, and in the districts of Ertso-Tianeti, Dusheti, Manglisi, and Marneuli. Thus, Dika was distributed where the soft winter wheat was not grown. These were generally mountain regions. As regards a Dika-soft wheat mixture, it is of great importance because it gives the grain better baking quality. A

barley-Dika mixture is also known for its good performance under high-mountain cold climate conditions, where Dika followed barley, which used to ripen earlier; at this time, the barley, being much smaller in stature than Dika, occupied the first tier, while Dika the second tier of the sowing. This enabled to make the sowing thicker, without interference of the two crops. The bread baked from the flour of this mixed crop outperformed in quality the barley bread. One more mixture – wheat-rye, should be mentioned here, which was widely distributed within Samtskhe-Javakheti, where rye frequently infested wheat crops. This gave an impetus to Georgian farmers to produce such a mixture intentionally. In this case, rye occupies the second tier, because it is higher than wheat.



Photo 2. *Triticum carthlicum* Nevski (Dika).

The bread with specific flavour and taste used to be baked from the wheat-rye mixture flour. Both the soft wheat and Dika were found in the wheat-rye mixture, all this is an evidence of great keenness of observation and practicality of the Georgian farmer. This is not a simple mechanical mixture but rather represents a competition between the wheat and rye varieties in nutrient uptake from the soil, as well as of water and light, the result of which, in addition to a competition between these two crops, is also their successful cohabitation. Despite the fact that Dika wheat was so widely distributed in Georgia, today it is critically endangered. The practices of mixed-sown crops have also been forgotten. One reason is the unjustified, sometimes forcible migration of the mountain population to lowland regions. The other one is the preferential livestock development of

cattle breeding in highlands at the expense of plant cultivation reduction. However, it is known that the full-value development of cattle breeding in isolation from field crops cultivation is practically impossible.

The Association Elkana has propagated the Dika wheat in farmers' fields in Samtskhe-Javakheti. Unfortunately, the 2009 adverse weather conditions fully destroyed wheat crops within the area up to 1000 m asl., while at the altitude of 1300-1400 m asl, the wheat developed well. Such climate anomalies continued in 2010 and will probably continue in the future against the background of the global warming. Therefore, Dika sowings should be moved farther up beyond 1200 m asl.

Triticum durum Desf., durum wheat (Tavtukhi, Photo 3): By its distribution and importance, this wheat ranks third in Georgia and second in the world. Several alternative views regarding the durum wheat distribution in Georgia exist. According to V. Menabde, the old-local Georgian Dika wheat was a result of divergence of the Near East durum wheat under mountain conditions. This opinion is also evidenced by the durum wheat seed remains discovered as a result of archaeological excavations in Kvemo Kartli, dating back to the fifth millennium BC. And concerning the distribution of the term 'Tavtukhi' in the Georgian language, it coincides with the fact of second introduction of durum wheat from the West Asia. It is exactly at this time, the 17th century, when Persia started to settle the Turkmen Qizilbash tribes in Kvemo Kartli. The distribution scope of Tavtukhi in Georgia is relatively restricted geographically and vertically as well. It is a lowland zone (400-800 m asl.) crop. The main distribution area of Tavtukhi in Georgia comprises the Bolnisi-Marneuli-Gardabani districts in Kvemo Kartli. Its distribution within other districts is insignificant. The so restricted area of Tavtukhi can be explained by the fact that the territory suitable for its distribution is sown to soft winter wheat varieties that outperform Tavtukhi by their quality characteristics – adaptation to the environment, yield capacity, and bread-baking quality. At present, the durum wheat is critically endangered in Georgia, with the exception of small area where the black-bearded durum wheat (var. *apulicum* Körn.) is grown in Kvemo Kartli.

Triticum compactum Host., club wheat (Kondara, Chagvera, Nagala Puri, Photo 4): It is a phylogenetic form close to soft wheat, and some wheat taxonomists (Menabde, 1948) classify it as soft wheat. This variety should rank among the oldest wheats of Georgia, because its remains were

discovered as a result of archaeological excavations in Kvemo Kartli, dating back to the sixth millennium B.C. In spite of the above, the wheat does not have economic importance in Georgia, therefore it is rarely can be found in pure sowings, although in some districts (Tetritskaro, Dmanisi), its pure sowings are also found. Morphologically the wheat strongly resembles the soft wheat, differing by having a compact spike (head). Hence its name - *T. compactum*. Despite insignificant economic importance, its botanical diversity is rather wide. Its 11 varieties are known in Georgia. In Meskheta the variety 'Tashbashi' is known, which is also found in Kartli. The variety is considered mountain wheat and is generally found within the soft wheat sowings in mountains. Being higher than the soft wheat, it occupies the second tier of the sowing. As a result, the sowing is rather thick and its yield is relatively higher.



Photo 3. *Triticum durum* Desf., durum wheat (Tavtukhi).

Triticum turgidum L., (English wheat, Photo 5): The wheat belongs to a 28-chromosome durum wheat group. Locally, it is mainly found as a mixed crop in the sowings of *T. durum*. Up to 12 varieties of the English wheat are registered in Georgia. The plant is characterized of high stalk (100-170 cm), average-sized, sometimes branched spike/head; the number of flowers per spikelet makes 5-7; the grain is flinty, white and red. In the 1950s, its sowings were found in Lechkhumi and Abkhazia, near Gagra, in small quantities – also in Samtskhe (Adigeni district). A branchy-eared variety of the English wheat – 'Kakhuri Datotvili' has been developed but its distribution failed. The English

wheat has lately come into the focus of attention of triticologists. It is considered one of the key species in the modern genetic classification of the wheat. In particular, it comprises most tetraploid wheats (Löve & Löve, 1985; Singeren et al., 1984; 1994). In spite of its great intraspecific diversity, the wheat does not have economical importance.



Photo 4. *Triticum compactum* Host., club wheat
 (Kondara, Chagvera, Nagala Puri).



Photo 5. *Triticum turgidum* L., English wheat.

Triticum polonicum L., (Polish wheat, Photo 6): Polish wheat is locally found as a mixed crop within Tavtukhi fields. Its pure sowings are registered in Shida and Kvemo Kartli (V. Menabde, 1948; N. Ketskaveli, 1957). The Polish wheat has a very attractive original spike, especially noticeable are its long (3.5cm) hulls. Its grains are of glassy consistence. The wheat is poorly distributed in Georgia, its only 3-4 varieties being found in Georgia. The Khorasan wheat - *T. turanicum* Jakubz. (P. Zhukovskiy, 1923; Udachin, 1979) is registered in Georgia. The var. *odsissianum* (Zhuk) Udach. was described by Zhukovskiy (1923). This wheat is widely distributed in our neighbouring countries (Armenia, Azerbaijan, and Turkey). Supposedly, it should have been widely represented in Georgia as well.



Photo 6. *Triticum polonicum* L., Polish wheat

Hulled wheat Species

Triticum monococcum L., cultivated einkorn (Gvatsa Zanduri, Photo 7): Cultivated einkorn is diploid, 14-chromosome hulled wheat, characterized of wide distribution area. In Georgia, it was distributed both as pure sowings and in the coenosis with Chelta Zanduri. The Georgian cultivated einkorn was divided into two morpho-ecological types by Menabde (1948). These are the West Georgian einkorn - *Proles colchicum* Men. – is characterized of strong development (gigantism) and is adapted to the Kolkheti humid environment, and the East Georgian einkorn - *Proles heothinum* Flaksb. – are relatively weakly developed, xerophilic, i.e. better adapted to dry environmental conditions.

Out of 4-5 varieties distributed in Georgia, one - var. *hornemannii* is present in Zanduri cenosis.

Other varieties are found both as pure sowings and as mixed crops in the durum wheat sowings. It is to be noted that the spikes of var. *hornemannii* frequently contain two-grained spikelet, which can be indicative of its bridging forms to Chelta Zanduri (*T. timopheevii* Zhuk.). Worthy of mention is a high content of protein of Gvatsa Zanduri, exceeding sometimes by 50% than of soft wheat. Also high is content of indispensable amino acids – phenylalanine, tyrosine, methionine, and isoleucine. These amino acids play a great role in the metabolism of human nerve cells. For example, phenylalanine and tyrosine participate in the synthesis of dopamine, noradrenaline, adrenaline and octopamine; these substances improve the human nervous system stability, contribute to the concentration of human spiritual strengths in terms of maintaining sobriety and stress relief. In addition to these substances, the einkorn contains the so-called yellow pigment – carotene, which is known for preventing rectal cancer. The bread baked from the einkorn flour has the hazelnut taste and flavor, which greatly improves the bread quality. The antioxidant carotene contains vitamin A. Thus, the cultivated einkorn is of many dietary uses, especially in Europe, where it is much valued and priced. It can also be used as animal feed. Earlier, its stalks, as the wholesome and strong material, were used in Georgia to cover roofs of various buildings. The stalks were also used as a binding/tying material, for stuffing mattresses, filling up various hollows, basket weaving and cap knitting.



Photo 7. *Triticum monococcum* L., cultivated einkorn (Gvatsa Zanduri).

Triticum dicoccum Schuebl., cultivated emmer (Aslim Photo 8): Emmer is the ancient hulled wheat. It was widely distributed in Asia, Europe and Africa. It is reputed to be the first cultivated wheat that originated from wild emmer (*T. dicoccoides* (Körn) Schweinf. F.Kornike 1888; A. Aaronsohn, 1906; G. Schweinfurth, 1908 et al) growing wild in the Fertile Crescent of the Near East. According to Vavilov (1931, 1935) and E. Sinskaya (1955), these two species originated in parallel from one common ancestor. Of interest is the opinion of Gorgidze (1968) that the soft emmer originated by mutation from the Colchian emmer - *T. paleocolchicum* Men., whereas Kuckuck (1964) believed that it originated from the Georgian cultivated emmer Dika - *T. carthlicum*. In Georgia, emmer was sown in the mountain area of East Georgia, within both the Greater and Lesser Caucasus Range. Because of its adaptability to cold mountain climate Emmer was sown in the places, where other crops could not perform. It is the spring wheat noted for its resistance to diseases and drought. Its grain protein content makes 23%. It is used for making bread, gruels, as animal feed. Emmer has been critically endangered in Georgia. It has been preserved only in one place: the village Didi Gomareti of Dmanisi (Beridze et al. 1989). In 2000, Elkana received the germplasm from village Gomareti consisting of two varieties var. *farrum* Bayle & var. *rufum* Schuebl.



Photo 8. *Triticum dicoccum* Schuebl., cultivated emmer (Asli).

Triticum paleocolchicum Men., (Kolkhuri Asli, Photo 9): Kolkhuri Asli, or Colchian Emmer, is a narrow endemic species of Georgia. First (Supatashvili, 1929) it was ascribed to *T. dicoccum* var. *chvamlicum* Supat. For its distinct morphological traits, L. Dekaprelevich and V. Menabde (1932) transferred it to rank of a subspecies - *T. dicoccum* ssp. *georgicum* Dek.&Men.; while, after it had been discovered in the archeological excavation dating to the Neolithic Age, V. Menabde (1940) ranked it as the species *T. paleocolchicum* Men. According to Menabde (1940), it represents a living relict of the historical past. Kolkhuri Asli is the emmer wheat. It is frequently found in the ceonosis of Macha wheat - *T. macha* Dek.Men., although its pure sowings are also found (Supatashvili, 1929). It is characterized of a compact, flat spike with 4-5 floret-bearing spikelets, the number of which per spike makes 34-36. Out of the favourable traits of Kolkhuri Asli, mention should be made of its resistance to fungous diseases. Its grain protein content amounts to 18.8%, that of lysine – 2.9%. Its high quality gluten conditions good bread-baking properties. The species adapts well to humid climate of West Georgia, also performing well under dry, hot climate conditions of East Georgia. This evidences the suggestion of its wider distribution in Georgia in the earlier times and the fact of its preservation in West Georgia where, under humid conditions, it has successfully replaced the cultivated emmer. Menabde (1948) considers Kolkhuri Asli as the ancient initial species that has arouse from the proto-macha in the Neolithic. Kolkhuri Asli is a good starting germplasm for its important desirable traits (Naskidashvili, 1978, 1984).



Photo 9. *Triticum paleocolchicum* Men., (Kolkhuri Asli).

Triticum timopheevii Zhuk. (Zanduri, Chelta Zanduri, Photo 10): Thanks to its unique properties, Zanduri is the most important wheat. Of its unique properties, mention should be made of Zanduri's absolute immunity to both - diseases and pests. Wheat is known to be prone to numerous diseases and pest. Some fungus diseases (rusts, smut, powdery mildew, etc.) may lead to a 25-30% loss of the yield. After Zanduri, wheat had become known to the general public not only in Georgia but abroad as well (in 1932, when Zhukovskiy described and classified the wheat as *Triticum timopheevii*), the intensive utilization of the wheat as germplasm began. The initial information about Zanduri comes from Gldenstdt (1771-1773), then Georgi (1795-1800). They described Zanduri wheat as the cultivated einkorn - *T. monococcum*, which can be explained by the fact that this very variety predominated in Zanduri sowings. Later, when as a result of divergence, the share of *T. timopheevii* in the ceonosis had increased, arose a need to define their name. Locals used to name *T. monococcum* and *T. timopheevii* according to their spike shape - Gvatsa Zanduri and Chelta Zanduri respectively, while the cenosis retained its common name Zanduri; later (1958), a new (third) variety - *T. zhukovskiy* Men. & Er., was added to the ceonosis. In 1948, Menabde delineated the exact distribution area of this wheat, which looks as follows: the northern boundary of distribution goes along the Tsageri-Orbeli-Lailashi-Patara Oni line; the eastern boundary is Kvanchkara-Dghnori; the western – Tamakoni-Gordi-Mekhena-Dghnori. These sites are known as the wheat's exclusive distribution area. New varieties derived in crosses with the wheat in Australia, and America, such as Konly, Timsten, Timgalen, Timvera, Gabo, Bledzoe, Georgia 1123, etc., share Zanduri wheat's disease immunity traits. These varieties are also immunity donors and gave rise to numerous other varieties.

Another direction in wheat breeding with the active involvement of Zanduri wheat is the cytoplasmic male sterility (CMS) and fertility restoration. The ability of Zanduri wheat to produce a CMS line was demonstrated in 1962 by Wilson and Ross (1962). When crossed with soft and durum wheat species, the first line – Wilson (that gave rise to the new Wilson variety) was reported to possess Zanduri cytoplasm. Sterile analogs of the wheat with Zanduri cytoplasm are not distinct from the initial form. After studying many sources of CMS, the Zanduri cytoplasm was found to be most valuable among them. Within pollen fertility restorers, particularly in the chromosome 1A, two

fertility restoration genes - Rf1 and Rf2. are localized. Several fertility restoration genes are reported to be identified in the Zanduri wheat cenosis (Fedin, 1972). Zanduri restores fertility in the lines having its cytoplasm, but in no case of *Egilops*'. This fact evidences that Zanduri is free from *Aegilops* genes. The fact that Zanduri had a restricted distribution area in Racha-Lechkhumi is indicative of its specific use for food. Zanduri bread was generally baked during special events – to celebrate the occasion, and to treat guests of honour. Zanduri has many desirable economic traits and should therefore be more widely utilized in the future for producing high- immunity & grain protein varieties.



Photo 10. *Triticum timopheevii* Zhuk. (Zanduri, Chelta Zanduri).

Triticum macha Dek. & Men. (Macha, Photo 11): According to V. Menabde (1948), the term 'makha' is the term of basic meaning in the vocabulary of the ancient civilization nations, which, in his opinion, is confirmed by the Sumerian language data (Grozny, 1913). As it is found out, the word 'mah' means – dear, respected, and splendid. In the vocabulary of West Georgians, 'makha' has a polysemantic meaning. For example, in Samegrelo 'makha' means 'man', in Lechkhumi – 'wheat', in Svaneti – 'makhashi' (a populated place). In Lazika, the word 'mokha' was given to the very special wheat. Possibly, asserts Menabde, a divine cult was meant under the word 'makha'. The same Sumerians had grain goddesses. Menabde believes that 'makha' had also a totemic loading and that is the reason why it has preserved to our days. Menabde concludes that Makha wheat

represents a type of soft wheat of the Stone Age. It existed together with free-threshing wheats, the distribution area of which was in West Asia. Makha is brittle and needs to be harvested in two stages. First, using a special implement – a hand thresher known locally as 'shnakvi' ('shamkvi') – spikes were collected and then the stem was cut. In spite of being hulled, grains in Makha wheat spikelet are not so densely set as in other hulled wheats (Zanduri, Asli). Based on the above, Menabde (1948) asserts that Makha is the progenitor of soft wheat species which, after acquiring the Q factor – the easy threshing character and the rachis stability – it, as a result of anthropogenic selection, has developed into a modern bread wheat. Makha is noted for its varietal diversity (14 varieties). For this reason, Dekapreleovich (1954) divided it into two subspecies - ssp. *imereticum* and ssp. *tubalicum*. Makha is a winter wheat. Among its desirable traits are: adaptability to humid environments, rather high resistance to diseases and pests, ability to produce large biomass; it is less demanding to soils, has high stem; its grain protein content makes 18%; it has good bread-baking quality and good yield potential under conditions of a humid environment, where other wheats become susceptible to fungus diseases. Because of being the carrier of the RF genome, Makha also represents the restorer of fertility in hybrid forms possessing the Zanduri wheat cytoplasm (Kihana and Tsunewaki, 1966).



Photo 11. *Triticum macha* Dek. & Men. (Macha).

Triticum spelta L., spelt (Photo 12): This wheat species has a rather interesting history. It was described as far back as the 18th century by Linné and was considered as the species spread in West Europe. According to Flaksberg (1935), it was

developed by the Old Germanic tribes – Alemanians and Schwabians. However, spelt was also distributed in Spain Asturias (where it was threshed by means of a shnakvi-like implement, like in Lechkhumi), to a lesser extent in Switzerland, Belgium, Australia. In 1957-58, the German scholar Kuckuck during an expedition in Iran discovered many forms of spelt in the territory inhabited by Bakhtrians. After that, spelt was also found in the countries neighbouring Iran – Turkey, Azerbaijan, and Armenia, but was not yet found in Georgia. Although, N. Ketskhoveri (1957) describes a case evidencing that spelt was known in Georgia. In particular, one of German encyclopaedias belonging to the Georgian prince Ioane Bagrationi bears an inscription ‘asli’ made in the hand of its owner beside the picture of spelt. Spelt as the emmer wheat should certainly have been distributed in Georgia as well. In 1967, several spikes strongly resembling spelt in the spikelet morphology were found in fields sown to Tetri Doli wheat in the village of Nichbisi, Mtskheta district. The forms with such hulls are known as speltiforms. The obtained material used to be sown and observed during years on an experimental plot. As a result of observations, the spike was found to be difficult to thresh, its rachis – brittle; the spike itself is beardless, of light blue color. This wheat variety failed to be placed in a set of the existing varieties. Therefore, it was decided to name it according to the place where it was collected, that is Kartli – var. carthlicum, without the Latin binomial.



Photo 12. *Triticum spelta* L., spelt.

Some researchers (Melia, 1972) think that the origin of speltoid plants in soft wheats results from the Q-factor weakening and the q factor

strengthening. The spelt origin ways should be sought in the interaction of hexaploid wheats. There are known crosses between soft wheat and makha, during which speltoid forms are intensively segregated in the F₂ generations, which if subjected to purposeful selection, may end up with creation of new varieties. True, makha wheat has been preserved only in Georgia, however there is an opinion (Menabde 1971), and not ungrounded, that it should have been distributed within much larger territory, together with soft wheat and that their spontaneous intercrossing was taking place at a larger scope. For the people, for whom Makha is not a totemic plant, the cultivation of other varieties, spelt in this case, in a wider territory should not pose a problem. That is why Makha wheat and not spelt has been preserved in Georgia. However, why has it (spelt) been preserved in Europe? It is known that eastern peoples were moving westwards along the northern coasts of the Mediterranean Sea towards Spain. The territories through which this road went were exactly the places where these nations lived (Switzerland, Germany, and Austria) and where spelt was spread.

Triticum Zhukovskiy Men. & Er., (hexaploid Zanduri, Photo 13): This wheat is one of the youngest varieties discovered in the 20th century. Menabde (1958-59) isolated it from the Zanduri wheat ceonosis. For its morphological and biological characters, and then based on the identified number of chromosomes ($2n=42$), the wheat was classified as hexaploid Zanduri endemic to Georgia. *T. zhukovskiy* is very close to *T. timopheevii*. Its leaves and stem joints are bristly; the spike is long and relatively narrow. In terms of ecology, it resembles *T. timopheevii* for its ability to perform well in humid, cool foothill; its grain protein content makes 23.6%, that of lysine – 2.9%. The bread baked from its flour is noted for its quality and nutritional value. The wheat is also known for its good immunity. Zhukovskiy wheat arose through autopolyploidy of *T. monococcum* - Gvatsa Zanduri (V. Menabde, 1958, 1960; Gorgidze, 1968; Chkhaidze, 1969). According to them *T. zhukovskiy* includes six genomes of *T. monococcum* and its genomic formula is $AAAAAA=6A$. According to the research conducted by Tavrini (1963) and Upadhyaya and Swaminathan (1965), *T. zhukovskiy* is allo-hexaploid species and comprises genomes of *T. monococcum* and *T. timopheevii*. The same was stated by Bowden, 1959. This actually corroborates the opinion of Georgian triticologists regarding the characteristics of the Zanduri ceonosis and its being

free from the *Aegilops* genome. Both directions - autopolyploidy and allopolyploidy were taking place in the Zanduri cenosis, under conditions of Georgia, while people fixed this process through selection and divergence. If earlier three species made up one sowing, thereafter the Georgian agriculturist managed to isolate them according to the morphological and quality traits that were characteristic of these species. Thus, the origin of Zanduri cenosis species is closely connected with the creative and agronomic activity of the Georgian people.



Photo 13. *Triticum Zhukovskiy* Men. & Er., hexaploid Zanduri.

Utilization of wheat products in Samtskhe-Javakheti region, South Georgia

Wheat grains are used to prepare various authentic Georgian dishes – Korkoti (wheat gruel), Khalipapa (thin wheat gruel), various porridges and soups. Various nutrition dishes and cookies are made with the wheat flour and grains together with fat. There are water mills throughout the region where the local people mill their wheat harvest. There are also big stone mortars in rural households where the wheat grains are formed into Korkoti (grains without husks), which is used for preparing various dishes. Also, wheat grain is used to feed domestic animals, in particular, wheat grains are used as the poultry feed and the bran is used to supplement cattle feed. Grain is fed to livestock whole or coarsely ground. Straw is made into mats, carpets, baskets and used for packing material, and

cattle bedding. Samtskhe-Javakheti is known for dishes using local cereal crops. Wheat flour and grains are used in the local cuisine. Bread baking with the wheat flour has a long history in the region; many rural households still keep this tradition. A *purne* (bread oven) holds a special place in Samtskhe-Javakheti homes and is used to bake a variety of breads including *lavashi* (soft, paper-thin flat bread), *shoti* (Meskhetian holed bread), *kakala* (round bread made by dividing the dough into round pieces and cooking them on a thick stone), and *somin* (*somun* in Turkish is bread baked on a moderate fire and noted for longer shelf-life and freshness).

Dough is also used in cooking other local dishes such as *tatarberagi*, which is a flattened dough shaped like a butterfly and boiled in salty water, eaten with the addition of *matsoni* (yogurt), garlic, and onion roasted in melted butter; *bishi* and *fatirbishi* (dough fried in oil or cooked in melted butter); *lukhumi* (round pieces of soufflé-like paste roasted in oil or melted butter); *katmar*, a five-layer rolled butter pastry similar to Georgian *kada*; *sironi*, which are Meskhetian noodles eaten with *matsoni*. Another dough-based food is home-made macaroni, called *erishta*. A traditional Meskhetian dish is *khinkali*, ravioli-like boiled dumplings found all over Georgia, but here also stuffed with *apokhti* (goose or other meat cured and dried), seasoned with pepper and steamed.

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REVIEW ARTICLE

The vanishing wheat landraces of the Fertile Crescent

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Abstract

Genetic diversity of wheat landraces constituted a sizable portion of the mega diversity in the Fertile Crescent as a center of origin and of diversity of major crop plants. Following wheat domestication in the Fertile Crescent, early farmers developed diverse wheat landraces, and contributed to their evolution, enrichment, on-farm conservation and developed efficient seed exchange systems, and ensured the continued evolution and diversification of these landraces. For millennia, wheat landraces served as staples for food production in the Fertile Crescent and beyond; however, their use dramatically declined in the 2nd half of the last century and they were replaced by modern high-yielding cultivars. Wheat landraces are facing the risk of genetic pollution, and genetic erosion and extinction due to anthropogenic and natural causes, including climate change. Monitoring and reversing genetic erosion in wheat landraces are scientifically challenging, technically and logistically difficult, and require long-term dedication and extensive efforts of farmers and the public sector. This paper presents in-depth assessment of the status of the ‘vanishing’ wheat landraces of the Fertile Crescent, their vulnerability to predicted climate change, and proposes a strategy to give evolution a second chance to engage in reversing this trend and restoring the allelic richness of these landraces.

Key words: Climate change, Diversity, Fertile Crescent, Genetic erosion, Landrace

Introduction

The Fertile Crescent is the core of West Asia and the Mediterranean Basin, where dryland agriculture was “discovered” and was characterized by small-to-medium traditional subsistence farms dotting the mountains, hills, plains and drier regions of this part of the Old World. The interplay between several important factors, including farm size, number of fields, and land ownership are needed to understanding the historical and current farmer’s practices, the extensive germplasm farmers developed as landraces, and the complex farming systems adapted to specific eco-geographical regions and socio-economic sectors of the society. It is widely acknowledged (Brush, 1995; Jaradat, 1998; Brown et al., 2008; Hamdi et al., 2010) that a special plant community and an adaptive population initiated the first “Green

Revolution” in the history of mankind. Upon the domestication of crops and animals, this region was the most appropriate place to start agriculture where the landscape, the climate, the plant community, and the animals contributed to successful production of surplus food, trade relations, central governments, and the appearance of great civilizations (Ladizinsky, 1998; Zohary and Hopf, 2000; Charmet, 2011). The grass communities of the Fertile Crescent were richly stocked with a number of cereal species that were easy to domesticate (Zohary and Hopf, 2000), with wheat being the most important cereal which provided energy and protein to native populations over many centuries (Fig. 1; Map of the Fertile Crescent and geographical boundary of wheat domestication) . Eight species are considered as founder crops of agriculture in the Fertile Crescent; they include three cereals [einkorn (*Triticum monococcum*), emmer wheat (*Triticum dicoccum*) and barley (*Hordeum vulgare*)], three legume crops [lentils (*lens culinaris*), chickpeas (*Cicer arietinum*) and pea (*Pisum sativum*)], flax (*Linum usitatissimum*), a fiber and oil crop, and bitter vetch (*Vicia ervilia*), a forage crop (Zohary and Hopf, 2000). Durum wheat (*T. turgidum durum*) has been of great historical significance because it provided a range of sub-species that were cultivated widely across the

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globe for thousands of years (Feldman, 2001; Fuller et al., 2012). Durum wheat came into cultivation originally in the Damascus basin in southern Syria about 9,800 B.P. (Zohary and Hopf, 2000). Historically the Mediterranean basin is the most important region for production of durum wheat, being the most significant durum import market, and the largest consumer of products derived from this wheat (Akar et al., 2009; Hamdi et al., 2010).

Wheat farming communities in the Fertile Crescent, and later in the Eastern Mediterranean, contributed, for millennia, to the evolution, enrichment, and on-farm conservation of diverse wheat landraces (Fig. 2a; image of Noorseh durum wheat landrace from Jordan, and Fig. 2b; image of Tabasi bread wheat landrace from Iran), and developed efficient seed exchange systems to ensure the continued evolution and diversification of these landraces (Zeven, 1999; Fuller et al., 2012). Farmers developed and utilized diverse wheat landraces to meet the complexity of a multitude of spatially and temporally diverse agro-ecological systems and to provide reliable sustenance and a sustainable food source to local communities. Landraces were the main focus of agricultural production in developing as well as developed countries until the turn of the last century with the arrival of formal plant breeding (Harlan, 1975); they have been developed mostly in environments with low natural fertility, dry or

semi-dry climates, and were adapted to drought and low input cropping systems (Dencic et al., 2000; Carvalho et al., 2013). The plant genetic resources conservation and utilization literature is replete with information on attempts at defining and identifying crop landraces (Camacho Villa et al., 2006). Nevertheless, misunderstandings regarding the correct identification and documentation of landraces persisted in both scientific (Brush and Meng, 1998; Bayush and Berg, 2007a; Berg, 2009; Newton et al., 2010) and popular literature and in gene bank records (Hammer et al., 1999; Bettencourt, 2011; WIEWS, 2012). If a landrace 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” (Camacho Villa et al., 2006), then a precise identification of a landrace will be a challenging endeavor (de Carvalho et al., 2013; Jaradat, 2006). The objectives of this paper was to review the status of the ‘vanishing’ wheat landraces of the Fertile Crescent, their vulnerability to predicted climate change, and proposes a strategy to give farmers and the natural environment a second chance to engage in reversing this trend and restoring the allelic richness of these landraces for the benefit of mankind (Newton et al., 2010; de Carvalho et al., 2013).

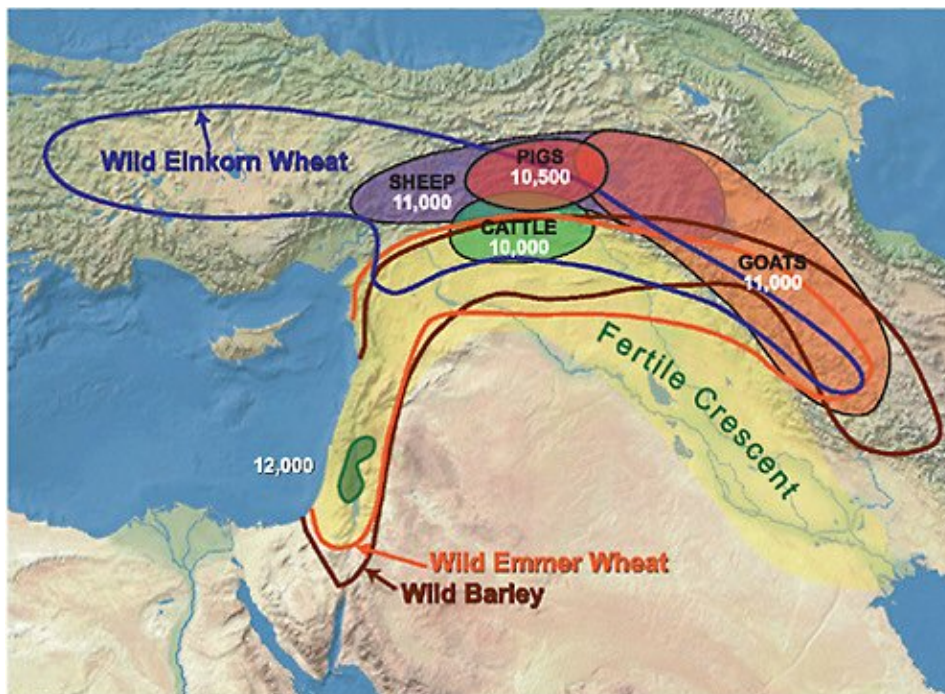


Figure 1. Map of the Fertile Crescent showing the geographical boundaries of wild emmer wheat, the immediate progenitor of most cultivated wheats, in addition to the wild einkorn wheat, wild barley and farm animals. (Google Earth, 2013)



Figure 2a. Image of Norsee durum wheat landrace from Jordan (Courtesy I. Rawashdeh)



Figure 2b. Image of Tabasi bread wheat landrace from Iran (A. A. Jaradat).

Early origins of Fertile Crescent wheat landraces

Diversification has been the most successful and widespread strategy of agricultural innovation and survival over the past 10,000 years (Feldman, 2001; Harlan, 1975; 1977; 1981). The development, selection and improvement of wheat landraces in the Fertile Crescent comprised a substantial part of this strategy (Bellon, 1996; Aderajew and Berg, 2006). Landraces of durum wheat evolved under arid and semi arid Mediterranean environments, through the long process of domestication, and natural and conscious selection. It is highly likely that plant traits conducive to development, adaptation, and survival depended drought prone Mediterranean environment are available in these land races (Mohammadi and Amri, 2013). The spread of durum wheat across the Mediterranean Basin from the Fertile Crescent occurred via Turkey (8,500 B.P.), the Balkan Peninsula, Greece

and Italy (8,000 B.P.), and from the Nile Valley to North Africa and the Iberian Peninsula (7,000 B.P.) (Feldman, 2001; MacKey, 2005). Traditional agroecosystems developed in the Fertile Crescent represent accumulated experience of the interaction with the environment and served as laboratories from crop germplasm evolution, dynamic conservation and sustainable utilization (Brush, 1995; Bayush and Berg, 2007b). Farmers' seeds are most often lumped together in one broad category called 'landraces'. But such a category covers variety types that reflect different levels of farmer involvement. Those differences matter when we discuss such issues as genetic erosion, on-farm conservation and seed related policies. The term landrace can be traced to the time when 'modern' varieties of cereals were introduced to European farmers in the late nineteenth century (Frankel and Hawks, 1975; Hammer et al., 1999). However, a century after warning of the consequences of the disappearance of landraces for the future of plant breeding, subsistence farmers continue to cultivate and sustainably conserve and use some of the original highly diverse germplasm pool of wheat landraces (Bellon, 1996). Numerous gaps in the knowledge about the origin and genetic structure of wheat landraces only allow us to theoretically anticipate the extent of their genetic erosion. Monitoring genetic erosion in landraces is scientifically, technically and logistically difficult, and requires long-term commitment and substantial efforts of different institutes (Harlan, 1975; FAO, 1998; Hammer et al., 1999).

A wheat landrace is composed of genetically heterogeneous populations comprising breeding lines and hybrid segregates which have evolved over many generations in contrasting environments and different local farming systems (Allard, 1990; Jaradat, 2013; Mohammadi and Amri, 2013). Genetic erosion of wheat landraces due to replacement with high yielding cultivars could devastate future sustainability of cropping in centers of origin by reducing the diversity available for future farmer-mediated crop evolution, as well as reducing diversity available for future breeding efforts in the wheat-growing parts of the world (Newton et al., 2009; 2010;). Wheat landraces of the Fertile Crescent, typically characterized by tall plants, long coleoptiles, and early vigor, provide early groundcover which is vital to weed suppression; this trait provides a competitive advantage over early emerging weeds and increased resistance to hand weeding operations in traditional

production systems (Jaradat et al., 1996; Moragues et al., 2006a; Rawashdeh and Rawashdeh, 2011). Traditional management of wheat landraces contributed more to the conservation of a general level of diversity than to the conservation of genetically stable and distinct populations. Therefore, a wheat landrace is far from being a stable, distinct, and uniform unit; its diversity is linked to the diversity of the material sown in its immediate geographical area, and to the level and frequency of seed exchange among farmers (Moragues et al., 2006b).

Current status of Fertile Crescent wheat landraces

Up until the mid 1900s, wheat landraces constituted a dynamic and indispensable component of the overall agricultural biodiversity, especially in the Mediterranean Basin, which has been largely valued as a source of agronomic, physiological, and genetic traits that can be used in scientific breeding programs and to improve the productivity of new wheat cultivars. During the 1970s and 1980s, and in many developing countries within and outside the Fertile Crescent, wheat landraces have been displaced by newly developed high-yielding cultivars. A number of International Agricultural Research Centers (IARCs) of the Consultative Group on International Agricultural Research (FAO, 1998; Mazid et al., 2013; Mohammadi and Amri, 2013) working within the Fertile Crescent promoted and encouraged the adoption of new wheat cultivars with higher yield potential at the expense of adapted landraces and old cultivars. On the other hand, these landraces were rarely cultivated in developed countries because of their comparatively lower yield potential and susceptibility to diseases when compared with high-yielding cultivars under high external input farming systems (Kebebew et al., 2001; Moragues et al., 2007). However, landraces and old cultivars out-yield, and have better quality attributes than, high-yielding cultivars under organic and low-input farming systems (Koç et al., 2000; Moragues et al., 2006c; Rawashdeh and Rawashdeh, 2011).

Wheat landraces have been largely displaced by high-yielding cultivars in many developing countries and are rarely cultivated in developed countries because of their low yield potential and susceptibility to diseases when compared with high-yielding cultivars under high external input farming systems. However, landraces and old cultivars out-yield, and have better quality attributes than, high-yielding cultivars under organic and low-input farming systems. Currently,

wheat landraces, as an underutilized but valuable genetic resource in contemporary agriculture, are gaining increasing importance. However, a major part of their diversity is conserved, but not fully utilized, in a network of gene banks around the world. The gene bank at ICARDA, Syria, maintains a total of 34,983, 75 % of which are landraces (See Figure 3 for more information on gene bank holdings of wheat landraces; Bettencourt, 2011; WIEWS, 2012; Figure 3).

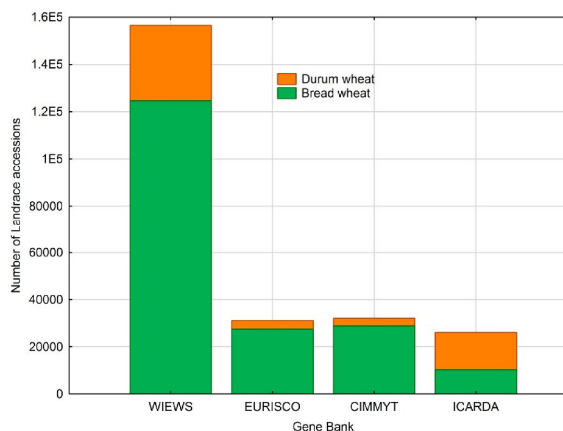


Figure 3. Number of durum and bread wheat landrace accessions conserved ex situ in major gene banks (data collated from several sources, see: Bettencourt, E. 2011).

Sources of information on existing germplasm collections. Crop GeneBank Knowledge Base. Available from

http://cropgenebank.sgrp.cgiar.org/index.php?option=com_content&view=article&id=658.

Population Structure of the Fertile Crescent Wheat Landraces

Plant accessions of wheat landraces or old varieties have complex structures, are characterized by their plasticity, are adapted to local agro-ecological conditions and their diversity can be increased by farmers' seed exchange (Ladizinsky, 1998). From a genetic point of view, regulatory genes played a central role in development of the initial domestication syndrome of wheat; whereas structural genes were more important during subsequent selection for trait diversification and the development of wheat landraces (Ladizinsky, 1998; Fasoula, 2004).

The present genetic structure of and the changes within wheat landraces were largely shaped and determined by traditional cultures and local cropping systems. Wheat landraces are considered as complex, variable, genetically dynamic and diverse populations in equilibrium with both biotic and abiotic stresses in their

environment (Zeven, 1998; Harlan, 1981; Camacho Villa et al., 2006). The genetic structure of wheat landraces is an evolutionary approach to survival and performance, especially under the arid and semi-arid growing conditions of the Fertile Crescent, in particular, and the Mediterranean Basin, in general (Ladizinsky, 1998; Hammer et al., 1999; Moragues et al., 2007). The combined effects of natural and farmer selection over thousands of years have led to an architecture of genotypes representing different combinations of traits, such as growth habit, cold, heat or drought tolerance, early growth vigor, competition with weeds, disease tolerance, water and nutrient use efficiency, time to heading and maturity, grain filling duration, and quality traits suited for diverse sustenance objectives and local food preferences (Zeven, 1998; Harlan, 1981; Kebebew et al., 2001; Camacho Villa et al., 2006).

The complex genetic structure of wheat landraces may have been strengthened over many generations of broadcasting the seed during planting time which exposed the seed to natural selection for adaptation. The seed are extensively mixed during harvesting, threshing and winnowing operations; therefore, there is a strong probability of more adapted and productive individual plants being relatively better represented in the new population of the landrace at the end of each cropping season (Kebebew et al., 2001; Bishaw et al., 2010; 2011; Newton et al., 2010; Jaradat, 2013). Consequently, farmers were able to manipulate, if not change the phenotypic composition of their wheat crops from generation to generation. Sowing stimulated unconscious selection for traits like none-shattering; whereas, changes caused by unconscious selection prompted observant farmers to practice intentional selection. Farmers found out that intentional selection for one trait often affected other traits as well, through linkage or pleiotropy (Ladizinsky, 1998; Newton et al., 2009). Historically, traditional management of wheat landraces contributed more to the conservation of a general level of diversity than to the conservation of genetically stable and distinct populations. Therefore, a wheat landrace is not a stable, distinct, and genetically and phenotypically uniform genetic resource; its diversity is linked to the diversity of other landraces grown in its immediate locality, and to the level and frequency of seed exchange among farmers (Frankel and Hawkes, 1975; Almekinders et al., 1994; Brown et al., 2008; Galiè, 2013). Knowledge about landrace genetic structure and phenotypic characteristics

plays a pivotal role in determining the structure and size of germplasm collections, as well as in the determining number of accession needed for regeneration and several aspects of quality control in order to avoid genetic erosion or drift (Hammer et al., 1999; Zeven, 2000; 2002; Motzo et al., 2004).

Evolution of wheat landrace populations may be hindered if the selection pressures select simultaneously in opposite directions; therefore, these landraces may not have the appropriate structure of their genetic variation in order to respond to multiple selection pressures at once (Brush, 1995; Ladizinsky, 1998; Brown et al., 2008). Nevertheless, wheat landraces may have an advantage over improved varieties in this regard since they tend to have relatively high levels of genetic diversity which could be a source of adaptive variation (Akar et al., 2009; Zeler et al., 2012). The genetic structure of landrace collections, when linked to geographical and environmental data, may reveal genomic indications of selection. This may constitute valuable information for breeding for specific environments, farming methods and end users (Reynolds et al., 2007; Newton et al., 2010).

Sustainable utilization of Fertile Crescent wheat landraces

Traditional subsistence and low-input wheat production systems in the Fertile Crescent, as compared with conventional systems, were more diverse at different levels, including landscape, field, soil, crop rotation, and crop. These systems placed greater emphasis on the integration of crop and livestock production on the farm. The high biodiversity of the traditional subsistence and low-input wheat production systems in the Fertile Crescent provided many ecological services that enhance farm resilience. Moreover, the long-term process of integrating biodiversity gains from traditional agronomic practices with genetic diversity at the wheat landraces level provided insurance against the impact of biotic and abiotic stresses on wheat yield and its quality (Dencic et al., 2000; Reynolds et al., 2007; Carvalho et al., 2013). Farmers in the Fertile Crescent acted as managers of food- and commodity-producing ecosystems and contributed through local food production to reduction of greenhouse gas emissions along the food supply chain, and to food security and environmental health and protection for millennia. From an energetic point of view, changes in consumption patterns are particularly important for countries in the Fertile Crescent; the

region that gave sedentary farming to the world is considered as the most food-deficit (Zohary and Hopf, 2000). Grain yield, food and bread quality, marketability, grain color, and grain size were among the most important traits for which wheat landraces have been developed in the Fertile Crescent (Blum et al., 1987; Motoz et al., 2004; see Figure 4). In addition, straw yield and quality were valued for their use as livestock feed, fuel and for old-style house maintenance purposes (Brush, 1995; Bayush and Berg, 2007a; 2007b;). Wheat landraces, based on their nutritional value, when locally-produced can contribute to lower greenhouse gas emissions (0.1 g CO₂ per calorie) as compared to rice (0.43 g CO₂ per calorie), or vegetables (0.57 g CO₂ per calorie). This may encourage local food production and promote food security, farmers' livelihoods, and eventually rural development (Ludwig and Asseng, 2006; Jaradat, 2013).



Figure 4. Image of spikes (top) and seed (bottom) of Noorseh durum wheat landrace from Jordan (Courtesy I. Rawashdeh).

Agronomic and nutritional quality attributes of Fertile Crescent wheat landraces

Rainfall and temperature in the Mediterranean environment are unpredictable, resulting in inconsistent environmental conditions for wheat growth and large genotype by environment interactions. A combination of multiple genotypes within a wheat landrace and different levels of agronomic traits contribute to yield stabilization under stress conditions (Kiær et al., 2009); however, yield traits conferring drought tolerance may incur yield penalties under optimal environmental conditions and when external inputs are available; whereas traits conferring maximum productivity are usually fully expressed in the absence of stress. A large number of agronomic and socio-economic studies indicated that farmers' selection for desirable agronomic and quality traits was a major force that shaped the dynamics of wheat landrace populations in the Fertile Crescent (e.g., Brush and Meng, 1998; FAO, 1998; Bishaw et al., 2010, 2011). Therefore, sustained on-farm conservation and sustainable utilization of these wheat landraces ensured, for thousands of years, their continued evolution and contribution to sustainable local food systems (Frankel and Hawkes, 1975). Increased yield stability attributed to the inherent heterogeneity of landraces under traditional low input agricultural systems in the Fertile Crescent can be ascribed to the fact that, regardless of the varying biotic and abiotic stress each plant is subjected to, a few or several genotypes within the landrace population will yield satisfactorily (Zeven, 1998; Kiær, 2009).

Durum wheat landraces, in particular, have been developed and evolved under low nutrient availability in the drier parts of the Fertile Crescent (RHarlan, 1977; Jaradat et al., 1996; Jaradat, 2006); therefore, they may provide a rich source for selection of genotypes adapted to low fertilizer input. In addition, these landraces may be of special importance for the uptake of nitrogen in nitrogen-limited environments due to their late maturity and their high nutrient use efficiency and ability to translocate more nitrogen into the grain than modern wheat cultivars. These landraces have the capacity for larger pre-anthesis uptake of nutrients, especially nitrogen, and their buffering capacity due to their large vegetative biomass (Dencic et al., 2000; Carvalho et al., 2013).

Grain protein content, protein quality, and seed color (especially yellow pigment), as well as, rheological properties, are the major nutritional quality attributes in wheat used in several foods in the Fertile Crescent and the Mediterranean Basin.

Gluten composition and strength are major factors that influence durum wheat quality; Mediterranean landraces retained a wide range of genetic diversity for gluten composition that has been mostly lost in modern cultivars (Dencic et al., 2000; Hamdi et al., 2010; Mohammadi and Amri, 2013). Macro- and micro-nutrient contents are important factors in determining the semolina quality because of their association with bran impurities (Rijal, 2010; Rawashdeh and Rawashdeh, 2011). These nutritional quality attributes are influenced by genetic and environment variables, such as temperature and rainfall, as well as soil fertility and nitrogen availability. Farmers selected for nutritional quality of domesticated wheat in the context of other crops that have been evolving simultaneously in the Fertile Crescent, such as lentils and chickpeas (Ladizinsky, 1998; Zohary and Hopf, 2000). The largest variability for quality traits was found in wheat landraces from the eastern Mediterranean basin (ie., closest to the Fertile Crescent) (Harlan, 1981). A second group, however, with lower level of variability, was landraces from the western Mediterranean basin; the latter differed from the former in grain weight.

Farmers in the Fertile Crescent generally believe that their wheat landraces have better nutritional value than modern high-yielding varieties, a perception supported by chemical analyses and quality testing (Motzo et al., 2004). However, research is needed to determine whether it is the nutrient content, bioavailability, or digestibility of the final product (e.g., bread, bulgur, frekeh, semolina, pasta, etc.) that makes products from wheat landraces more filling and nutritious (Koç et al., 2000). Research programs aiming at improving wheat landraces need to address farmer concerns about nutritional and quality attributes of their landraces. For example, selecting and breeding for wheat end-products with shorter cooking time or longer shelf life, are of particular importance to farmers and consumers alike.

Genetic erosion of the Fertile Crescent wheat landraces

An estimated 75% of the genetic diversity of crop plants was lost in the last century (FAO, 1998; Hammer et al., 1999), wheat landraces in the Fertile Crescent were no exception (Bettencourt, 2011; WIEWS, 2012). Farmers acknowledged (personal observations) the disappearance of some landraces of all crops, including wheat, and attributed this loss, in part, to limited public efforts to multiply their seeds within the existing formal and informal seed production systems. In addition, many farmers

abandoned the age-old tradition of maintenance selection and their landraces became vulnerable to genetic erosion (Hammer et al., 1999; Harlan, 1975; 1977). Genetic erosion is one of the major factors that are still contributing to the decrease in cereal diversity, in general, and wheat diversity, in particular. Genetic erosion refers to the permanent reduction in richness or evenness of common localized alleles or the loss of combination of alleles over time in a defined area. Both components of genetic diversity, i.e., the number of different alleles and their relative frequencies, are taken into consideration (Kebebew et al., 2001; Moragues et al., 2006c).

Genetic erosion of wheat landraces in the Fertile Crescent, and elsewhere in the Middle East, was caused by a number of anthropogenic and natural interacting factors. Apart from the consequences of genetic erosion, the particular combination of genes in a well-adapted landrace, if lost, may be difficult or even impossible to reconstruct. The gradual loss of Fertile Crescent wheat landraces coincided with the introduction of high-yielding and genetically more uniform cultivars, and resulted in a severe threat to the world's long-term food security (Brush, 1995; Jaradat et al., 1996). Although neglected for a long time since the advent of high yielding cultivars, the need remains urgent to conserve and utilize the large genetic diversity in the remaining landraces, whether being sustainably utilized in subsistence farming systems at a limited scale (Rijal, 2010; Mazid et al., 2013) or stored in gene banks (Bettencourt, 2011; WIEWS, 2012), as a safeguard against unpredictable demographic, or climatic stressors (Hammer et al., 1999). The inclusion of landraces, including those in the Fertile Crescent, in international treaties (FAO, 1998) and national decrees may protect their genetic integrity and enhance their sustainable use and conservation in their local environments for future generations. However, despite earlier predictions about a total loss of these and other landraces (Zeven, 1998) in centers of origin and centers of diversity, some landraces persisted and became scattered in subsistence farming systems throughout the Fertile Crescent and the larger Mediterranean Basin (Bayush and Berg, 2007b; Newton et al., 2010; Jaradat, 2013).

This persistence can mainly be attributed to their ability to occupy a special niche in traditional and subsistence farming systems, their increased stability and buffering capacity under changing climates, their ability to resist or withstand biotic

and abiotic stresses, and inter-genotypic competition and compensation. In addition, there are other opportunities for safeguarding such landraces and preventing their total loss. Research results indicated that some wheat landraces may grow very well in new habitats and can be adopted in new cropping systems, where their culinary qualities are in demand, or where farmers' options are limited (Brush and Meng, 1998; Akar et al., 2009).

On-farm conservation of wheat landraces of the Fertile Crescent

Several agronomic and socio-economic studies in the Fertile Crescent (Brush, 1995; Dencic et al., 2000; Jaradat, 2006) and other centers of wheat diversity (Bishaw et al., 2010; 2011; de Carvalho et al., 2013) indicated that farmers' selection for desirable agronomic and quality traits was a major force that shaped the population dynamics of wheat and other cereal landraces; therefore, continued and sustained on-farm conservation and sustainable utilization of these landraces will ensure their continued evolution and contribution to sustainable local food systems (Rijal, 2010; Mazid et al., 2013). On-farm conservation is the sustainable management of genetic diversity of locally developed traditional crop landraces (and cultivars), as well as their wild progenitors and weedy relatives within traditional agricultural systems. On the other hand, on-farm sustainable utilization provides a natural laboratory for evolution to continue and help a gradual build-up of plant traits imparting adaptation to eco-geographical regions and to meet the requirements and needs of local communities. If the progress that has been made so far on the methodologies for on-farm conservation of wheat and other cereal landrace genetic diversity was not satisfactory (Jaradat et al., 1996; Hammer et al., 1999; Mazid et al., 2013); then the perennial question of whether a need remains for on-farm conservation of landraces under the unfolding socio-economic conditions in plant genetic resource management and conservation. From the farmers' point of view, the merits of wheat landraces are adaptation to local eco-geographical and socio-economic conditions, besides yield stability. However; this is not sufficient justification for continued cultivation once higher yielding varieties became available, especially during the first decade of the "Green Revolution." The current situation in the Fertile Crescent is similar to the historic experience in the early years of the 20th century Europe (Zeven, 2000; 2002). European efforts to conserve cereal

landraces on farm during the pre-World War II period failed. On-farm conservation of landraces was largely not possible and resulted in massive loss of age-old valuable genetic resources. However, these developments triggered an interest in and a pioneering effort to explore, collect, document and utilize landrace germplasm from the gene-rich parts of the Old World, such as the Fertile Crescent, Mesopotamia, and Ethiopia (Harlan, 1975).

The factors affecting genetic diversity of wheat landraces at the eco-geographical level were found to affect and shape the genetic differentiation at the molecular level; therefore, it is possible to make inferences about the relative role of selection and population differentiation when comparing patterns of population genetic differentiation at the quantitative traits (Q_{ST}) and molecular markers (F_{ST}) levels. These genetic principles suggested that on-farm conservation of landraces by farmers differs in important respects from *in situ* conservation of their wild relatives (e.g., einkorn or wild emmer wheat, both of which are distributed with the Fertile Crescent). A landrace has generally been selected to suit the environment in which it is cultivated and to satisfy the particular needs of its growers, such as flavor, seed color, protein content and gluten strength, and cooking qualities. Landrace conservation on-farm requires continuation of the farmer-induced selection processes through which these landraces have been developed and their genetic structures were shaped. The traditional knowledge and practical skills that accompany these processes are crucial to on-farm management and improvement of landraces for food and agriculture.

The maintenance, use and development of plant genetic resources on and near farms offer many opportunities to combine genetic observation with agricultural development. On-farm conservation, which is a dynamic form of plant genetic resources management, allows the processes of natural and artificial selection to continue (Aderajew and Berg, 2006; Hamdi et al., 2010). A number of initiatives are suggested to strengthen on-farm management of wheat landraces, and to improve farmers' livelihoods; these may include: support and improvement of farmer selection of landrace varieties; improved links between gene bank and on-farm conservation activities; increased use of landraces that meet farmers needs from gene bank collections; promotion of on-farm seed production by farmers and support for informal seed exchange between farmers; and, where appropriate, modification of policies to support rather than

penalize on-farm conservation and management of landraces (Zeven, 1999; 2002; R Galiè, 2013).

On-farm seed management of wheat landraces in the Fertile Crescent

Farmers have developed seed management practices leading to the formation of landraces, and at a later stage, of old (or folk) varieties (Brush and Meng, 1998; Berg, 2009; Galiè, 2013), through experiences that are determined by the biological characteristics of a particular crop and the developing farm technology. This explains why both landraces and old varieties may have existed in the same community depending on the crop type and the availability of appropriate technology (RHarlan, 1975; 1981; Jaradat et al., 1996; Kebebew et al., 2001).

Traditionally, farmers' seeds were usually lumped together under the name 'landrace'; a broad category which prevents clear-cut definitions and making it difficult to describe farmers' seeds with sufficient accuracy. Such accuracy is needed especially where and when issues such as genetic erosion (Bayush and Berg, 2007a), on-farm conservation (Brush, 1995; Bayush and Berg, 2007b) and seed-related techniques (Galiè, 2013) and policies (FAO, 1998) are concerned. In subsistence and traditional farming systems, on-farm seed management is largely a family business where male and female farmers have traditional roles in planting, harvesting, cleaning, selecting, storing and processing seed and grain at different points of the production and consumption cycle (Bishaw et al., 2010; 2011; Mazid et al., 2013).

Seed selection, in the field as plants, or after threshing as seed, is pragmatic through critical observation of one or more family members. Farmers observe and evaluate crop performance in the field; they inspect and evaluate plant, spike and seed size, shape and color as selection criteria whether for own consumption, sale in the local market, or as seed for the next planting season (Bishaw et al., 2010; 2011; Mazid et al., 2013). In selecting seed for the next planting season, farmers adopted a dynamic process, thus adapting their landrace(s) to a changing management practices, market demand, and climatic conditions (Zeven, 1999; 2000; 2002). Wheat subsistence and resource-poor farmers in the Fertile Crescent and elsewhere in the Middle East (e.g., Ethiopia) used primitive plows, broadcast the seed, harvest by sickle, thresh with oxen or horses and manage the harvest as bulk. These farmers acted as wheat agronomists and breeders and contributed to the

evolution of complex and diverse landraces they and their forefathers managed (Harlan, 1977).

Historically, and during the long history of wheat landrace emergence and evolution, farmers practiced seed replacement and/or seed renewal (Zeven, 1999; Aderajew and Berg, 2006). However, some farmers tended to keep their own seed for many years (>20), presumably due to its food quality attributes (Rijal, 2010; Galiè, 2013). A decision to replace seed of a particular landrace may be attributed to a perceived reduction in its productivity after many years of planting under unfavorable management or environmental conditions. Another possible reason may arise from genetic changes (e.g., mechanical seed mixing) or deterioration in quality (e.g., bread making quality or kernel hardness). However, more often, farmers tend to obtain fresh seed stocks of the same landrace from other farmers or the local market, as a measure of seed renewal. Farmer-to-farmer seed exchange is as old as wheat farming itself and continued for millennia to be the major initial source of wheat seed, especially of landraces and old varieties (Almekinders et al., 1994; Aderajew and Berg, 2006; Mazid et al., 2013); this process contributed to a wide global distribution of wheat (FAO, 1998) long before the advent of the commercial seed industry (e.g., Turkey Red in the US, Red Fife in Canada). Seed obtained from neighbors, relatives or local market made up the majority of sources of landrace seed in the Fertile Crescent (Bishaw et al., 2010; 2011; Mazid et al., 2013) and other parts of the Mediterranean Basin (Moragues et al., 2006c; Mohammadi and Amri, 2013). Nevertheless, saved seed by farmers remained the main source of seed for the next planting season in the Fertile Crescent; besides the farmer's confidence in the quality of own seed, this age-old practice ensured availability of accessible seed at the right time and place; and saved on expenses at the critical time for planting.

The seemingly low rate of seed replacement in subsistence farming communities may stem from unawareness of the availability of, or access to improved landrace seed produced, for example, using participatory plant breeding (Fasoula, 2004; Galiè, 2013EF). These factors may delay farmers' access to high quality seed and possible adoption of new and improved landrace germplasm; with a possible negative impact on local economy. Traditionally, farmers passed on the indigenous knowledge of seed management and its qualities, along with landrace seed itself, from generation to generation and among farmers even over relatively

long (>100 km) distances (Mazid et al., 2013; see below). However, the once dominant culture of traditional form of seed exchange and trade in rural areas of the Fertile Crescent gave way to commercial seed industry in large parts of the region, to the formal public seed sectors (i.e., cooperatives) in a few countries (e.g., Syria Jordan, and Iraq), or already lost altogether (FAO, 1998).

Farmers, while managing, processing, and trading or exchanging seed, usually distinguished between seed and grain of wheat landraces. Free, in-kind, or low-cost exchange and trade of wheat seed among farmers has been the bases to maintaining diversity in wheat cropping systems, as well as a guarantee for food security in subsistence farming (Bishaw et al., 2010; 2011; Mazid et al., 2013). This exchange was based on cooperation and reciprocity, and involved the sharing and exchange of ideas and knowledge, as well as culture and heritage throughout history and across large distances (Kebebew et al., 2001). The unfortunate large-scale loss of local wheat landraces along with the local knowledge about their different qualities and uses can be attributed to the gradual disappearance of small farmers and local food cultures in large parts of the Fertile Crescent. The unrealistic split, by the seed industry, of the nature of seeds as production tool and product, and the transformation of a common resource developed by farmers into a commodity had numerous biodiversity, economic and social repercussions. The transformation, in a relatively short period of time, of a self-regenerative resource into an input under the full control of the private seed industry, starting with parent selection for planned crosses to the delivery of seed bags at the farm gate, changed the nature of the seed and of agriculture itself in centers of origin and diversity, such as the Fertile Crescent. Finally, in the context of farmers right to intellectual property of their landrace seeds and their knowledge about it, the FAO Resolution 5/89, for example (FAO, 1998), defined Farmers' Rights as "rights arising from past, present, and future contribution of farmers in conserving, improving and making available plant genetic resources, particularly those in centers of origin and centers of diversity". In addition, the International Treaty on Plant Genetic Resources for Food and Agriculture also recognized these rights, and stressed the protection of farmers' traditional knowledge and sharing of benefits, and suggested ways through which national governments can promote such rights.

Indigenous knowledge of the Fertile Crescent wheat landraces

Indigenous knowledge about wheat landraces (and their wild relatives), as well as the native plant communities, traditional management practices, are invaluable resources in our search for new and applicable methods of conserving and using biodiversity, in general, and wheat genetic resources, in particular (Jaradat, 1998). Unfortunately, little is known and documented about farmers' criteria for selection, and their age-old knowledge has only recently been recognized and used in participatory plant breeding (Motzo et al., 2004; MacKey, 2005; Galiè, 2013) and in biodiversity conservation (Jaradat, 1998; Mazid et al., 2013). Documentation and acknowledgment of indigenous knowledge are critical to retaining the innumerable benefits of centuries of keen observation on the functioning of agro-ecosystems, characteristics of different cultivated crop plants, and on their multiple uses. In view of the climate change, the indigenous knowledge systems will be valuable to integrate the impact of long-term climatic and biological changes over many centuries (Brush, 1995); an important objective in the Fertile Crescent where farming is not a marginal economic activity for many subsistence and resource-poor farmers, but also a vital social and environmental endeavor.

Current knowledge about the information embedded in seed of landraces may not constitute a new invention; it is, to a large extent, the result of cumulative and collective discoveries upon which additional discoveries may be based in the future. Therefore, we should acknowledge a 10,000 year long, unbroken thread of expertise and knowledge that is derived from growing and managing diverse landraces for food while at the same time, consciously or unconsciously, preparing and improving them for future generations (Hammer et al., 1999; Aderajew and Berg, 2006). Farmers' ability to modify the gene frequencies of their landraces was exemplified by generating wheat germplasm to fit the ever changing environmental conditions and evolving management practices, and by integrating their "breeding" methodologies with indigenous knowledge.

The traditional farming systems in the Fertile Crescent (e.g., wheat-based, barley-based, mixed farming, etc.) were as important as the germplasm itself in the development, maintenance, evolution and improvement of wheat landraces (Zeven, 2002). Wheat landraces persisted in the Fertile Crescent primarily because of farmers' ability to dynamically manage their farming systems (Jaradat

1998). Mixtures of diversified local field crops enabled farmers to select adapted germplasm to fit local farming systems and environmental conditions. Wheat landraces may persist alongside modern wheat varieties if they are characterized by distinctive traits that make them relevant in the farming system or demanded in the market. On-farm conservation of landraces can be encouraged by means of interventions in the farming and seed supply systems (Rijal, 2010; Mazid et al., 2013).

The cultural and aesthetic significance of a landrace, its gastronomic values, biotic and abiotic tolerance or resistance properties, shape the knowledge those communities in the Fertile Crescent accord to the seed, the plant it produces, and to the final product consumed by these communities. Traditionally, women were, and to a large extent still are, the custodians of seed security, diversity and equality, as well as the prime depositories and disseminators of indigenous knowledge about the quality and methods of food processing and preparation (Bishaw et al., 2010; 2011; Mazid et al., 2013). Many traditional Mediterranean foods are made from durum wheat, mostly by women. These include frekeh, bulgur, pasta, couscous, and flat bread. More recently, however, the gradual loss of indigenous knowledge at the local level can be attributed to limited interest of young men and women to invest and work in agriculture and to live in rural areas.

Predictive characterization of Fertile Crescent wheat landraces

The key components of wheat landrace population diversity include richness, size, spatial distribution, and population differentiation (Allard, 1990; Dencic et al., 2000; Hamdi et al., 2010). The distribution of population sizes determine whether a wheat landrace is characterized by a single large population, many small populations, or several populations of more or less similar sizes. Population distribution is a measure of the spatial aggregation of populations and how it can affects the delivery of ecosystem services, such as genes for qualitative (e.g., disease resistance) and quantitative (e.g., drought or salinity tolerances) biotic and abiotic stresses (Hammer et al., 1999; Kebebew et al., 2001; Jaradat, 2006).

Predictive characterization using spatial analysis of wheat landraces was suggested to predict which wheat landrace germplasm might have desired quantitative or qualitative traits. Wheat landrace populations found in pests and diseases hot spots are most probably have accumulated necessary alleles and evolved

resistances over time. Therefore, these populations might be predicted to harbor genes or gene complexes for biotic stress resistance (Dencic et al., 2000; Jaradat, 2006; Carvalho et al., 2013). Also, if an association can be established between genetic diversity and rainfall, it may allow the extrapolation of the potential impacts of climate change on wheat landrace diversity when empirical data on predictive climate models, particularly rainfall, are available. This information would be useful in developing conservation measures to mitigate the effects of genetic erosion through climate change (Hammer et al., 1999).

Population differentiation (i.e., genetic diversity partitioned within and among populations of a landrace) has implications for the conservation of genetic resources of wheat landraces and their ecosystem service purposes (Ludwig and Asseng, 2006). More genetic variation within landrace populations might confer greater elasticity in the face of climate change; whereas, genetic differentiation among populations may be associated with different types or levels of a given ecosystem service. The relationship between environmental heterogeneity and genetic diversity, in general, and genetic differentiation within and among populations, in particular, is not well characterized except in a few cases; nevertheless, the distribution of genetic diversity is known to be influenced by or associated with climate, soils, vegetation, and elevation variables (Moragues et al., 2007; Reynolds et al., 2007; Mohammadi and Amri, 2013). Therefore, it will be possible to indirectly predict the potential impact of climate change on the distribution of genetic diversity in centers of origin and diversity of wheat landraces, and to locate landrace populations with specific or wide adaptation for a particular biotic or abiotic stress.

Conclusions

Wheat farming communities in the Fertile Crescent contributed, for thousands of years to the development and conservation of wheat landraces. They developed efficient seed exchange systems to ensure the continued evolution and diversification of these landraces to meet their needs and to provide reliable sustenance and a sustainable food source to local communities. The present genetic structure of, and the changes within, these landraces were largely shaped and determined by traditional cultures and local cropping systems. The combined effects of natural and farmer selection have led to landraces with combinations of traits, such as growth habit, cold, heat or drought tolerance, early

growth vigor, competition with weeds, disease tolerance, water and nutrient use efficiency, time to heading and maturity, seed filling duration, and quality traits suited for diverse sustenance objectives and local food preferences. Historically, traditional management of wheat landraces contributed more to the conservation of a general level of diversity than to the conservation of genetically stable and distinct populations. Therefore, a wheat landrace is far from being a stable, distinct, and uniform; its diversity is linked to the diversity of other landraces grown in its immediate geographical area, and to the level and frequency of seed exchange among farmers. The landraces identified as threatened by genetic erosion in this study are valuable sources of traits for adaptation to marginal wheat-growing parts of the world with high temperature and salinity, and may have specific traits to combat climate change. Wheat landraces constituted, until recently, a dynamic and essential component of the overall agricultural biodiversity of the Fertile Crescent, in particular, and the Mediterranean Basin, in general. This biodiversity was valued as a major source of traits that have been used in scientific breeding programs and to improve the productivity of new wheat crop cultivars. This agricultural biodiversity, arguably, can make a far greater contribution to increase wheat productivity and the sustainable delivery of a more secure food supply in the Fertile Crescent, the most food-deficit region of the world.

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