Chapter 4
Characterisation of Genetic Diversity in Wheat Landraces

Özlem Özbek

4.1 Introduction

Wheat is the most revolutionist crop in the world, because it resulted in conversion of our hunter-gatherer ancestors to sedantic societies, who became traditional farmers around 10,000 years ago. The other revolution in the history of wheat was the domestication process, by which the brittle rachis of wild emmer (*Triticum turgidum* ssp. *dicoccoides* Körnick.) and *Triticum monococcum* ssp. *aegilopoides* evolved to non-brittle rachis of emmer wheat [*Triticum turgidum* ssp. *dicoccon* Schrank Thell. ($2n = 4X = 28$, *AABB*)] and einkorn wheat [*Triticum monococcum* ssp. *monococcum* ($2n = 2x = 14$, A^mA^m)], respectively. *Triticum monococcum* and *Triticum dicoccon* were the most popular crops until the early Bronze Age. Then, they started to be replaced by the high-yielding and free threshing wheat varieties (*Triticum aestivum* $2n = 6X = 42$, *AABBDD* and *Triticum durum* $2n = 4X = 28$, *AABB*). After domestication process, domesticated wheat varieties started to be cultivated by traditional farmers, and the seeds have been sown for thousands of generations since then. Although traditional farmers did not apply formal breeding programmes, selection was still under progress due to the natural selection in the environment and farmers' personal interest on the wheat varieties they grew. Farmers used these primitive relatives of wheat for their domestic uses such as feeding their livestock and home use for making bulgur, erişte (homemade macaroni) and so on. When they grow the wheat landraces, they made selections on the wheat varieties, they grown about their resistance to biotic and abiotic stress factors, and amount of the yield and yield stability in low input agricultural system (Zeven 1999). Until the last century, traditional agriculture has been some kind of heritage from generation to generation; therefore, the seeds have been sown for thousands of generations about 10,000 years ago. Those were called the wheat landraces, which

---

Ö. Özbek (✉)
Department of Biology, Faculty of Art and Science, Hitit University, Çorum, Turkey

N. Zencirci et al. (eds.), *Wheat Landraces*,
https://doi.org/10.1007/978-3-030-77388-5_4

were described as "variable plant populations adapted to local agroclimatic conditions which are named, selected and maintained by the traditional farmers to meet their social, economic, cultural and ecological needs" (Teshome et al. 1997) (see some other definitions in Zeven 1998). The landraces have enormous amount of genetic diversity covering unique genotypes enhancing their adaptability to different environmental conditions particularly to extreme conditions in remote mountainous places. The landraces grown on farms by traditional farmers have the opportunity to continue their evolution, which provides a dynamic and diverse genetic structure, and they can easily adapt to the changing environmental conditions in their habitats. The seed exchange system which is carried out by traditional farmers increases the genetic diversity and extend the germplasm of the landraces. The seeds can be exchanged between farmers, friends and neighbours in the same village or purchased from a commercial seed market (Zeven 1999). In the last century, the wheat breeding studies started and the new wheat varieties, which have high yield and adapted to specific environmental conditions, were developed and replaced the landraces. The wheat landraces germplasm has lost 75% of their genetic diversity (Jaradat 2013). Therefore, the extent of variability and the characterisation and partition of genetic diversity within the local germplasm collections are important criteria to determine the status of wheat landraces particularly for the future interests of their use and for the improvement and efficient genetic diversity maintenance and the utilisation of plant species (Desheva 2014). The wheat landraces were investigated for the characterisation of genetic diversity in terms of morphological, phenological and agronomic traits, proteins, enzymes and molecular aspects.

4.2 Variation in Morphological, Phenological and Agronomic Traits

Climate change causes the change in the environment in which all organisms live. The plant species could manage these new conditions through phenotypic plasticity and adaptation by natural selection or moving to find conditions to which they are used to (Nicotra et al. 2010). When a genotype is expressed differently, it produces different phenotypes in different environments called phenotypic plasticity (Bradshaw 1965 cited in Turcotte and Levine 2016). Thus, it is important to determine the different phenotypes, which are examined as variations in the morphological and agronomical traits which are due to the phenotypic plasticity or genetic diversity. The characterisation of morphological and agronomical traits is an important issue for estimating the genetic diversity in the natural, local and cultivated plant populations for the breeding programmes and agricultural demands.

The variation in morphological characters and agronomic traits was investigated in diploid, tetraploid and hexaploid wheat species and their landraces in the several previous studies. The agronomical traits studied are biological yield (BY), grain yield per plant (GYP), harvest index (HI) and yellow pigment. The morphological traits studied are the number of spikelet per spike (SS), the number of kernels per spike (NKS), the number of kernels per spikelet or fertility, plant height (PHt), tiller number (TN), number of tillers per plant, fertile tiller, 100-kernel weight (g) (HKW), 1000-kernel weight (TKW), peduncle length (PL) and spike length (SL), spike width (SW), awn length (AL), beard length (BL), upper node length (UNL), width of truncation (WT) and barb length (BbL, root length (RL), root fresh weights (RFW) and dry weights (RDW), shoot fresh (SFW) and dry weights (SDW), seed colour (SC) and seed shape (SS). The phenological traits studied are days to heading (DTH), days to maturity (DTM), grain filling period (GFP) and glume pubescence (GP).

*4.2.1 Einkorn Wheat (*T. monococcum *ssp.* monococcum*) Landraces*

Einkorn (2*n* = 14, *AA*) includes both wild and cultivated forms originated in Southeast Anatolia near Karacadağ (Heun et al. 1997). Wild einkorn *Triticum boeticum* is divided into single-grain *T. agilopoides*, and two-grain *T. thoudar* and *T. urartu*, while the cultivated einkorn is named as *Triticum monococcum* ssp. *monococcum*. *T. monococcum* has annual habit, 30–70 cm culm from the base to the upper end, indeterminate, bilaterally compressed spike with two rowed, 8–10 cm in length and awned. The spike disarticulates into the individual spikelets with rachis segments at maturity. The brittle rachis differentiates the wild einkorn from the cultivated einkorn (Stallknecht et al. 1996; Kimber and Feldman 1987).

There has been no much research interest in morphological or agronomical traits of einkorn wheat according to the previous studies. Variability in agronomic traits, sprouting, frost resistance, heading, maturity time, plant height, number of spikelets per spike, grain weight and TKW in einkorn (*T. monococcum*) landraces was evaluated. Einkorn landraces generally displayed late maturity and small seed prevalent character; thus, einkorn had limiting cultivation in many places all over the world, but in Metalliferous Mountains, it is still a common cultivar (Butnaru et al. 2003). The most relative variable agronomical character was the grain yield, followed by the spike length and the thousand kernel weight in a set of 15 einkorn wheat landraces, and cluster analysis indicated that the landraces were grouped into six groups (Uzundzalieva et al. 2016).

4.2.2 *Emmer Wheat (***Triticum turgidum** *ssp.* **dicoccon** *Schrank Tell.) Landraces*

The geographic distribution of genetic diversity and the population structure of tetraploid wheat landraces in the Mediterranean basin have also received relatively little interest. This is complicated by the lack of consensus concerning the taxonomy of tetraploid wheats and by unresolved questions regarding the domestication and spread of naked wheats. These knowledge gaps hinder the crop diversity conservation efforts and the plant breeding programmes (Oliveira et al. 2012). Emmer wheat cultivation has been drastically reduced during the last century as a consequence of replacement with the high-yielding wheat varieties. However, more recently, the increase in interest for the healthy foods, along with its agronomic and nutritive values, has caused an increase in the cultivation area, which is now more than 2000 ha (Pagnotta et al. 2005). Thirty-nine Italian ecotypes and cultivars of *Triticum turgidum* L. spp. *dicoccum* Schrank ex Schübler (emmer wheat) displayed a huge amount of diversity not only between varieties but also within the varieties according to agro-morphological and molecular analysis (Pagnotta et al. 2005). Former studies, on Italian (and foreign) emmer accessions, have been carried out to assess variation in the agronomic and quality traits by the morphological field evaluations (Damania et al. 1992; Piergiovanni et al. 1996; Galterio et al. 1998; D'Antuono and Minelli 1998), in order to select the material among the old landraces. The analysis of morphological characters (plant height, spike length, spike weight, distance between spikelets, number of spikelets per spike, number of grains per spike, number of grains per spikelets, grain length, thousand grain weight and weight of grain per spike) of a collection of Spanish emmer wheat lines indicated that there were seven different botanical varieties, which were less than previous records of ten, thus displaying a wide diversity (Alvarez et al. 2007). These kinds of studies are important for the future registration of the material, germplasm conservation and use of this valuable source of emmer germplasm for the future breeding programmes (Pagnotta et al. 2005).

4.2.3 *Durum Wheat (***Triticum turgidum** *var.* **durum** *Desf.) Landraces*

The morphological characters have correlations with some agronomical traits. Some morphological characteristics such as the number of spikelet per spike (SS), the number of kernels per spike (NKS), the number of kernels per spikelet or fertility, tiller number (TN), the number of tillers per plant, 100-grain weight (HGW) and 1000-kernel weight (TKW) positively correlated with agronomical traits such as biological yield (BY), grain yield per plant (GYP) and harvest index (HI) (Al-Ajlouni and Jaradat 1997; Jaradat 1991). Variation in these morphological traits will directly affect the agronomical traits, which are important for the agricultural production.

Variation in the morphological and agricultural traits in durum wheat landraces was analysed by comparing them with the commercial cultivated durum wheat checks. The reason for this was that the traits were superior in landraces to the commercial durum wheat varieties, which were determined to have been exploiting for the improvement of commercial varieties' germplasm as a genetic resource for future durum wheat breeding programmes. On the other hand, the traits, which the commercial durum wheat varieties were superior to landraces, might be considered to improve the landrace germplasm by crossing studies (Getachew et al. 1993).

The variation in the morphological, phenological and agronomical traits was reported in the durum wheat landrace germplasm from the different regions of the world in the previous studies.

The variation in glume colour, glume pubescence, spike density, spike length, seed colour, seed virtuousness, seed size, seed shape, beak length, spikelet per spike and seeds per spike in durum wheat landraces from four regions and five altitudinal gradients in northern and north-central regions of Ethiopia was used to estimate the genetic diversity. Most of the traits were found to be polymorphic, while monomorphism was common in many of the populations for the dense spike, long beak and glabrous glume. The highest mean diversity was observed for seed colour, seed shape and glume pubescence, whereas the spike density displayed the lowest diversity index (Bechere et al. 1996).

Seven tetraploid wheat populations from Shoa and Gojem Administrative Regions of Ethiopia were examined for variation of eight morphological characters (glume colour, glume pubescence, awn condition, awn length, awn colour, beak length, spike density and seed colour). Monomorphism was common for the awn length and glume pubescence in many of the populations, and the awn condition was found to be a fixed character in the entire collection, whereas the rest of the characters exhibited polymorphism in varying degrees. The lowest level of diversity was determined for glume pubescence (excluding awn condition). The analysis of variance of diversity for individual characters indicated that most of the variation was due to differences among the districts rather than among the populations within the districts such as the glume pubescence, which showed significant differences only among the districts. It might be considered for the future studies and that would be better if the study samples are collected from more different areas than having more samples from similar areas (Tesfaye et al. 1991).

Durum wheat (*Triticum turgidum* var. *durum* Desf.) landraces from the Syrian Arab Republic were characterised in terms of morphological characters (pubescence of leaves, spike density, spikelet attitude, glume colour, lemma colour, awn colour and glume hairiness) and agronomic traits (grain yield, straw yield, crop growth duration (days), spikes/m^2, seeds per spike, spike weight and 1000-seed weight). According to farmers' decisions, average grain yield was the lowest in western mountainous regions, while it was the highest with overestimated yield level in southern parts of the country, which displayed the tendency of landraces to produce more straw rather than grain dry matter under high rainfall conditions. Glume, lemma and awn colour were found to be highly variable, both within and among the landrace groups. The plants both with glabrous glumes and with pubescent glumes were observed in three landrace groups (Bayadi, Shihani and Surieh), while the other landrace groups were identified having only one form of glume hairiness. The yellow colour was the predominant colour for kernel in the groups, whereas the variation in spike density was clearly the first character to differentiate landraces. Distribution patterns of the various landrace groups indicated that only a few landrace groups were widely distributed and most others were regionally concentrated. The results indicated that Syrian durum wheat landraces had genetic diversification due to the heterogeneous nature of landraces and different landraces adapted to per region or village. However, durum landraces were found in mixture with *T. aestivum* at large proportions in the mountainous regions in the west of the country, where farmers prefer a species mixture (Elings and Nachit 1991).

Ethiopia is one of the countries where the wheat landraces are still growing. In a study, 34 tetraploid wheat (*Triticum turgidum* L.) landrace populations from four regions in Ethiopia were investigated to determine the diversity and distribution of these traits on the basis of administrative regions and altitudinal gradients for some morphological characters (glume colour, glume pubescence, beak awn, seed colour and spike density). All characters displayed polymorphism, except spike density, in all regions and most altitude groups. The highest variable character was seed colour and the lowest variable character was spike density. On the other hand, the diversity was increasing as with the increasing better climatic conditions and in optimal altitude ranges. All the result showed that the diversity has not changed considerably within the past 25 years or so, when compared to previous estimates (Belay et al. 1997).

The landrace genotypes of durum wheat from Jordan have been evaluated for 18 morphological- and yield-related traits (plant height, peduncle length, plant height ratio, spike length, awn length, awn/spike length ratio, the number of spikelets per spike, the number of seeds per spikelet, spike node, the number of seeds per main head, seed weight/main head, the number of tillers per plant, number of seeds per tiller, seed weight per plant, kernel weight (main head), kernel weight (tillers), kernel weight (average) and protein content). The study results indicated that the magnitude of phenotypic divergence in these landrace genotypes is large, especially when they are compared with a world collection of durum wheat. According to experimental evidences, the variation in altitude and long-term average rainfall of the collection sites gives rise to the phenotypic differentiation. The landrace genotypes are clustered into five groups on the basis of altitude and long-term average rainfall of collection site. Three canonical factors accounted for 92% of total variance in these clusters. The phenotypic diversity found in these landrace genotypes could help to identify genetically different genotypes for durum wheat improvement (Jaradat 1991). Mac Key (1966) noted the continuity of morphological traits among *T turgidum* convar., which is parallel in the morphological variation among the *T. durum* landrace groups to such an extent that clear distinction between groups could not always be made. The grouping should therefore merely be considered as a systematic description of visible variation.

4.2.4 *Bread Wheat (*Triticum aestivum *L.) Landraces*

Omani wheat landraces were analysed based on 15 qualitative and 17 quantitative characters and they displayed variations. Quantitative characters had higher diversity index ($H' = 0.66$) than qualitative characters ($H' = 0.52$) in tetraploid wheat, and 0.63 and 0.62, respectively, in hexaploid wheat. The morphological data showed that Omani wheat landraces had considerably high diversity and even simple morphological characters could be used for an effective characterisation of diversity in Omani wheat (Al Khanjari et al. 2008).

Fifty-three pure lines of bread wheat (*Triticum aestivum* L.) derived from seven landraces collected from southeastern Iran were analysed to determine genetic variation and heritability for 13 developmental and quantitative characters. The landrace genotypes displayed lower values for the number of grains per spike, 1000-grain weight, grain yield and harvest index, while they were late in days to heading and taller than the cultivars. On the other hand, some landrace genotypes showed similar grain yield with the modern cultivars, and for number of grains per spike, number of spikes per plant, 1000-grain weight and harvest index, they showed moderate to high genetic variation. Wheat landraces have genetic variation, which is an important source for agronomic characters. Therefore, the landraces with higher genetic variation for agronomical characters might be used for improvement of landrace germplasm by inter-crossing (Moghaddam et al. 1997).

In a previous study, it was reported that wheat (*Triticum* spp.) landrace populations were mixture of different tetraploid and hexaploid wheat species in Ethiopia. The tetraploid ($2n = 4x = 28$) wheat species were identified in mixtures of varying proportions of *Triticum durum* Desf., *Triticum turgidum* L., *Triticum aethiopicum* Jakubz., *Triticum polonicum* L. and *Triticum dicoccon* Schrank, and the hexaploid ($2n = 6x = 42$) wheat species was mixed with *Triticum aestivum* L., and *Triticum durum* was determined as the most predominant species, while the hexaploid *Triticum aestivum* was determined in nine populations from Wollo (Eticha et al. 2006).

Buerkert et al. (2006) revealed interesting results about the genetic composition of farmer's wheat (*Triticum* spp.) landraces from Afghanistan. They selected randomly 21 cereal fields on both sides of the Panjshir River in the upper Panjshir valley of northern Afghanistan. They surveyed morphological differences on morphological characters, and after that, they collected information about the field size and grain yield and a formal interview with the landowner on the cropping sequence and the inputs used. The results of morphological evaluation displayed that the collection included 19 taxonomically different varieties of bread wheat (*Triticum aestivum* L.); in addition, barley and triticale (*Triticosecale* Wittm.) were found in the mixtures. Farmers were not aware of morphological differences within these mixtures; however, they recognised their populations according to grain colour, cooking properties and resistance to mildew and frost. The most interesting thing about the result was the most widespread occurrence of *T. aestivum* var. *subferruginіnflatum*, which so far have only been reported together with var.

subgraecinflatum from Mongolia. The landrace populations were clustered into the different groups according to the cluster analyses based on the isozymes and agronomic data, which were the prime target of artificial selection and under the effects of different evolutionary forces.

The *ex situ* collection of common wheat (*Triticum aestivum* L.) landraces stored for more than 10 years in IPGR-Sadovo were analysed for the variation in the morphological and agronomic characteristics. The wheat landraces were characterised with the most relative variable character which was the spike length (C.V. % = 15.09%), followed with 1000-grain mass (C.V. % = 8.04%) and the number of spikelets per spike (C.V. % = 7.66%) (Desheva 2014).

4.3 Variation in Seed Storage Proteins

The seed storage or endosperm proteins offered great opportunity to reveal genetic variation within and between the populations of a species or interspecies. By means of seed storage, proteins, gliadins and glutenins which are also known as prolamins provide nutrients (amino acids) for embryo during germination of seeds (Ciaffi et al. 1993). The germplasm of wheat landraces at all ploidy levels was investigated in terms of seed storage proteins (gliadin and glutenin) and also for conferring their relationship with technological properties (Ciaffi et al. 1991; Ciaffi et al. 1992).

*4.3.1 Einkorn Wheat (*Triticum monococcum *L. ssp.* monococcum*) Landraces*

Einkorn wheat (*Triticum monococcum* L. ssp. *monococcum*) has only A^mA^m genome with $2n = 14$ chromosomes. The expression of HMW-glutenin subunits and gliadin proteins differs in diploid, tetraploid and hexaploid wheat species; particularly, the subunits encoded by *AA* genome decreased during the evolution of wheat. The screening of seed storage protein composition of Spanish-cultivated einkorn wheat (*Triticum monococcum* L. ssp. *monococcum*) indicated that three and up to six allelic variants were detected for the *Glu-A1*^{m} and *Glu-A3*^{m} loci, respectively, while 7 and 14 alleles were detected for the *Gli-A1*^{m} and *Gli-A2*^{m} loci, respectively, among the accessions analysed. The Spanish einkorn wheat collection displayed 48 different genotypes based on the origin, and seed storage protein compositions have been determined (Alvarez et al. 2006).

Evaluation of seed endosperm proteins (gliadins and glutenins) in Turkish-cultivated einkorn wheat (*Triticum monococcum* ssp. *monococcum*) landrace populations displayed great genetic diversity ($H_e = 0.65$). The gliadin proteins showed higher genetic diversity and allele combinations than HMW-glutenin proteins (Keskin et al. 2015). The increasing trend in the world as well as in Turkey is the great interest for healthy foods particularly organic farming products or food products produced by the local farmers. Turkish-cultivated einkorn wheat farming is the most popular crop landraces particularly in Bolu and Kastamonu provinces in Turkey recently. Its local name is “Siyez” and used to make bread, bulgur and pastry products such as cookies, savoury roll covered with sesame seed, etc.

A large germplasm collection, including *Triticum monococcum*, *T. boeoticum*, *T. boeoticum* ssp. *thauodar* and *T. urartu*, were investigated for their protein composition at the *Gli-1* and *Gli-2* loci (Ciaffi et al. 1997). The results indicated that *T. monococcum* and *T. boeoticum* were very similar in their gliadin patterns, and they were different distinctly from *T. urartu*, which was resembled to the *A* genome of polyploid wheats more than did *T. boeoticum* or *T. monococcum* in the gliadin pattern. The study confirms that *T. monococcum* and *T. boeoticum* are different subspecies of the same species, but *T. monococcum*, while it supports the hypothesis of *T. urartu*, is the donor of the *A* genome in cultivated wheats. Diploid wheat germplasm showed high level of variation for gliadin proteins, which might be further analysed as to whether the loci coding them have any linkage with the genes encoding for the desirable traits to determine parental candidates and to transfer alien genes into cultivated polyploid wheats (Ciaffi et al. 1997).

Einkorn and emmer wheat were the most popular cereal crops until the early Bronze Age, and they were replaced by high-yielding wheat varieties. The formal breeding studies speeded up the replacement of landraces with the modern bread wheat and durum wheat varieties, which are the products of breeding programmes. This replacement has caused a 75% loss of genetic diversity in the last century (Jaradat 2014).

*4.3.2 Emmer Wheat (***Triticum turgidum** *L. ssp.* **dicoccon** *(Schrank) Thell.) Landraces*

The cultivated emmer wheat was domesticated around the Karacadağ Mountain in the southeastern part of Turkey (Özkan et al. 2002; Özkan et al. 2005). Emmer wheat germplasm is important for revealing the domestication of wheat and for the improvement of modern wheat varieties due to its rich germplasm harbouring the high level of genetic diversity and different gene combinations. Polymorphism for gliadin proteins of Turkish-cultivated emmer wheat (*Triticum turgidum* L. ssp. *dicoccon* (Schrank) Thell.) populations was evaluated, and the results indicated that emmer wheat populations had great genetic diversities ($H_e = 0.92$) and showed 27 different patterns, which were the combinations of different gliadin proteins (Fig. 4.1). Most of the Turkish-cultivated emmer wheat populations had the α-45 and w-35 gliadins closely associated with dough quality; thus, emmer wheat germplasm is bearing the desirable traits related to quality. Pearson’s correlation analysis displayed that the latitude had strong influence ($r_P = 0.510$; $p = 0.026$ at <0.05%) on the genetic diversity estimates (Özbek et al. 2011).

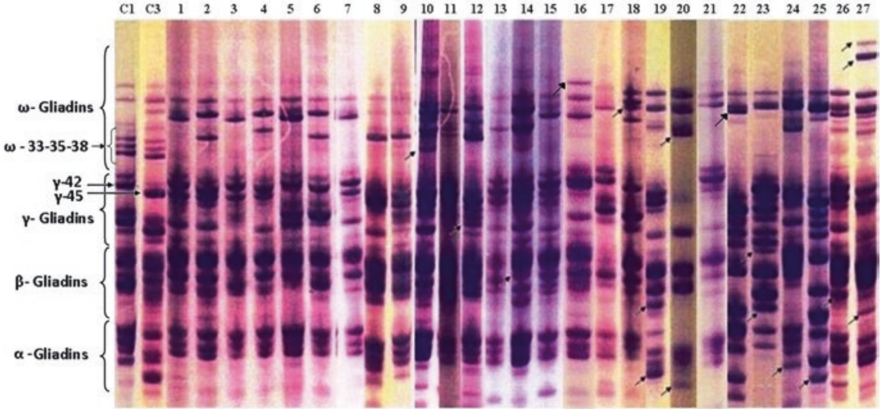

Fig. 4.1 Gliadin band patterns observed in Turkish emmer wheat populations. (Source: Özbek et al. 2011)

Glutenin proteins are part of seed storage proteins and are composed of two different types of protein groups according to their molecular weights as high molecular weight (HMW) and low molecular weight (LMW) glutenin subunits (Payne and Lawrence 1983). HMW-glutenin subunits have polymeric protein structures because of cross-linkages by disulphide bonds and rich in glycine residue in content (Payne and Corfield 1979).

Investigation of genetic diversity in Turkish emmer wheat landrace populations collected from different provinces in terms of HMW-glutenin proteins indicated that the mean values of expected heterozygosity (gene diversity) and average heterozygosity among the populations were estimated as 0.31 and 0.12, respectively. On the other hand, actual genetic differentiation (*D*) reveals that the partition of genetic diversity was between 24% and 76% within populations. These results infer that emmer wheat landraces are well adapted to the different environmental conditions and have dynamic evolutionary history still in progress. The results of this study showed the significant influence of ecogeographical variables on HMW-glutenin diversity (Özbek et al. 2012). The band patterns of HMW-glutenin subunit of a Turkish emmer wheat population from Kastamonu province are given in Fig. 4.2.

4.3.3 Durum Wheat (Triticum turgidum *var.* durum *Desf.) Landraces*

A collection of *Triticum durum* wheat comprising 25 cultivars from different regions in Iran and 10 cultivars from different European countries were investigated in terms of HMW-glutenin subunits. In the collection, HMW-glutenin subunit 1 encoded by *Glu-A1* was not detected, while the prevalence of the null allele (52%)

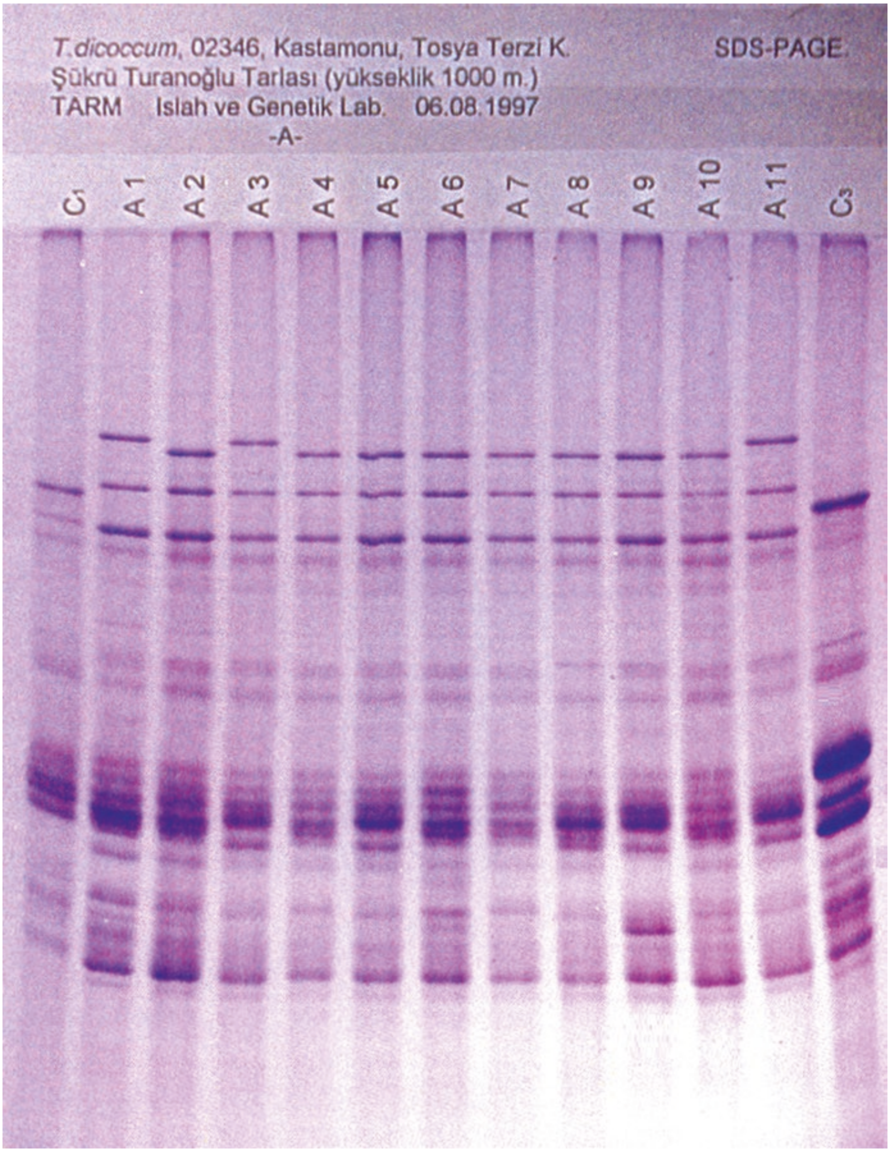

Fig. 4.2 High molecular weight glutenin subunits band patterns observed in Turkish emmer wheat population from Sinop province. (Photo by Özbek Ö., 2006)

and 2* subunit (48%) at the *Glu-A1* was observed. For *Glu-B1* locus, about 80% of the alleles composed of 14 + 15 (32%), 13 + 16 (28%) and 7 + 20 (24%) in the Iranian durum wheat compared to European durum wheat (Motalebi et al. 2007).

Iranian durum wheat (*Triticum turgidum*) landraces presented higher frequency for HMW-glutenin subunit in the null allele as reported in Iranian bread wheat

(*Triticum aestivum* L.) landraces (Kamali et al. 2011). This might be related to the existence of bread wheat, which took place in the area including Iran. Therefore, null allele is the common and the most frequent allele in both durum and bread wheat landrace germplasm. The allele number observed for *Glu-A1* and *Glu-B1* loci was 3 and 11 alleles, respectively. Iranian durum wheat landrace germplasm might have different combinations of HMW-glutenin subunits, and this might be considerable for breeding programmes particularly for improving pasta-making quality (Naghavi et al. 2009).

Anatolian durum wheat “Kunduru” landrace germplasm displayed high polymorphism in terms of gliadin and glutenin proteins. In the expense of high-yielding wheat varieties, wheat landraces are neglected, and many of the landraces are under extinction risk from the local farmers’ fields. Therefore, the studies on the landraces are revealing the importance of maintaining and conserving these valuable genetic resources (Alsaleh et al. 2016).

*4.3.4 Bread Wheat (*Triticum aestivum* L.) Landraces*

The electrophoresis profiles of HMW-glutenin subunits in some of the Iranian bread wheat (*Triticum aestivum* L.) landraces displayed null allele which was the predominant compared to subunits 1 and 2* at the *Glu-A1* locus, while *Glu-B1* locus displayed higher allelic variation as 7, 7 + 8, 6 + 8, 14 + 15, 7 + 9, 17 + 18, 13 + 16 and 20. The highest and the lowest frequencies were observed for the subunits 7 + 8 (56%) and 13 + 16 (2%) at *Glu-B1* locus and 2 + 12 subunits (74%) and the rare 2*** + 12′ (2%) subunits at *Glu-D1* locus, respectively. Based on Payne scoring method, three landraces were identified as superior. It sounds that Iranian wheat landraces have high variation for the quality traits and HMW-glutenin subunits and present potential sources for the desirable quality traits to be used in bread wheat breeding programmes to improve bread-baking quality (Kamali et al. 2011).

Terasawa et al. (2009) investigated variations in the morphological characters and HMW-glutenin subunit composition of an Afghan wheat collection maintained in Kyoto University together with 65 accessions of Iranian and Pakistani wheat. The higher frequencies were observed for the alleles encoding for HMW-glutenin subunit of *Glu-A1c* (encoding subunit null), *Glu-B1b* (7 + 8) and *Glu-D1a* (2 + 12). The Afghan wheat landraces represented typical morphological characters of landraces, and for the genetic diversity in terms of HMW-glutenin subunits and AFLP molecular markers, they had equal to or lower than neighbouring countries and lower in Afghan wheat landraces, respectively. The results of the study displayed the existence of a decrease in the genetic diversity in Afghanistan wheat landraces.

4.4 Variation in Isoenzymes

Analysis of diversity in terms of isozymes and agronomical traits in ten tetraploid wheat landrace populations from different localities in the central highlands of Ethiopia indicated that the variation observed within populations was higher than between populations. The differentiation between populations was not high among the populations which were attributed to the landrace populations who were sharing a common ancestral population and/or adaptation to similar climatic conditions. The pattern of genetic divergence was determined as independent from geographic distance. The landrace populations were clustered into the different groups according to the cluster analyses based on the isozymes and agronomic data, which were the prime targets of artificial selection and under the effects of different evolutionary forces.The clustering based on the agronomic traits resulted in the populations grouping together due to the similar agronomic performance. Therefore, taking more samples within a locality or population would be a better approach to capture the range of variation in the landrace populations of the central highlands of Ethiopia (Tsegaye et al. 1996).

*4.4.1 Emmer Wheat (*Triticum turgidum *L. ssp.* dicoccon *(Schrank) Thell.) Landraces*

Isoenzymes are important tools for the characterisation of genetic diversity in the natural and cultivated cereal crops. Turkish emmer wheat landraces were investigated by means of three isozyme (endopeptidase-1 (*Ep-1*), aminopeptidase-1 (*Amp-1*) and aminopeptidase-2 (*Amp-2*)) systems, and considerably high level of genetic diversity ($H_e = 0.23$) was estimated and eco-geographical variables had significant influence on genetic diversity of isoenzymes in Turkish emmer wheat populations according to statistical analysis (Özbek et al. 2013).

Isoelectric focusing (IEF) polyacrylamide gel electrophoresis is a method used for the analysis of isozyme diversity, which provides important information about the evolutionary history of plant species. The tetraploid wheat landraces (*Triticum dicoccon* Shrank, *T. turgidum* L., *T. durum* Desf., *T. pyramidale* Percival and *T. aethiopicum* Jakubz.) grown in Ethiopia were investigated to determine the genetic diversity in terms of α-amylase isozymes and to get inferences about the evolutionary histories of Ethiopian wheat landraces. Two zymogram types, band 18 (*α-Amy-B1*) and band 1 (*α-Amy-B3*), of the malt types were identified in *T. dicoccon*, while in the rest of the landraces, four zymogram phenotypes were identified. The overall results displayed that the genetic diversity was low in cultivated tetraploid wheats from secondary centres for α-amylase isozymes, which might be due to the founder effect or selection. It is supposed that among the tetraploid wheat species, *T. dicoccon* was the first wheat arriving to the Ethiopian highlands ca. 5000 years ago. It is contradictory whether the feral type Ethiopian tetraploid wheat landraces are direct descendants of *T. dicoccon*, or were introduced independently.

The feral types and *T. dicoccon* were sharing common α-amylase zymogram pattern band 1 that is showing the gene flow between them (Belay and Furuta 2001).

Landraces have desirable traits, which can be exploitable for improvement of wheat varieties or developing new wheat cultivars. In previous studies, it was reported that emmer wheat germplasm has some desirable traits such as resistance to the leaf diseases and common bunt (Corazza et al. 1986), resistance to yellow rust (Damania and Srivastrava 1990), powdery mildew (Jakubziner 1969) and Fusarium head blight or scab (Oliver et al. 2008).

4.4.2 *Durum Wheat (*Triticum turgidum *var.* durum *Desf.) Landraces*

The genetic diversity has been analysed between origins, and within origins, of a durum wheat world collection according to 13 isozymes. The comparison of the isozyme frequencies in wild emmer and durum wheat could provide the knowledge to understand the effect of domestication process. According to the origins, Iran, Mexico, Ethiopia, Egypt and Afghanistan had the highest genetic diversity for durum wheat. The geographical or political lines were the effective factors for the grouping of the landraces along within-variability of the origins. According to gene frequencies, Egypt might be considered a microcentre of diversity for durum wheat within the Mediterranean centre, although it is certainly related to Ethiopia, while Mexico has become a new microcentre of diversity, quite likely man-made, and is distant from other centres of durum wheat diversity (Asins and Carbonell 1989).

4.4.3 *Bread Wheat (*Triticum aestivum *L.) Landraces*

Analysis of five isozymes to determine the genetic diversity and genetic structure of 324 Chinese wheat landraces indicated that the landraces from the western part had higher diversity than from the eastern part, and populations were clustered into three major groups particularly neighbouring populations clustered together; the first group included most of the populations from western China and two populations from Xinjiang and Gansu and Ningxia, the second group included the northern populations from Mongolia to Japan and the third group consisted of the southeastern populations from Shaanxi, China and Japan. The results suggested that the Silk Road had important role through the transmission of wheat on both northern and southeastern populations. The genetic differentiation between eastern, northern and southern populations was determined as well, and it was reported in Korea and Japan (Ghimire et al. 2005).

Isozymes have functional roles in plant metabolism and they play differential activities in different parts and stages of plants. Esterase or peroxidase isozymes were investigated in both roots and shoots of seedling among landraces of wheat (*Triticum aestivum* L.) from Sichran. In root tissues, esterase had two isozymes, while peroxidase had single isozyme pattern and displayed no variation. Both esterase and peroxidase showed variation displaying 6 and 15 isozymes for shoots, respectively, and peroxidase had higher variation than esterase in shoots (Zuli et al. 1999).

The isozymic variation of *peroxidases*, *malic dehydrogenase*, *alcohol dehydrogenase*, *acid* and *alkaline phosphatase* were assessed in dry kernels and of *α-amylases* in germinating kernel endosperms, and of *phosphor-glucose mutase* and *isomerase*, *esterases*, *leucine aminopeptidase*, *glutamic oxaloacetic transaminase*, *malic dehydrogenase* and *peroxidases* in 15-day-old seedling leaves, were analysed. The overall results indicated that variation in isozymes analysed was not successful to identify the cultivars and classification based on the isozymes that did not infer the ancestor-descendant relationships among related cultivars (Salinas et al. 1982), because isozymes don't have high genetic variation.

4.5 Genetic Diversity

4.5.1 Einkorn Wheat (L. ssp. monococcum*) Landraces*

The diploid wheat *Triticum monococcum* L. (einkorn) was replaced by the high-yielding tetraploid and hexaploid wheat varieties and largely forgotten by the modern breeders. Einkorn germplasm was not subjected to breeding programmes; therefore, it was devoid of breeding bottlenecks, and it has conserved the genetic variation that existed during its domestication period (Kilian et al. 2007).

The molecular analysis based on the nuclear and chloroplast microsatellites of 50 einkorn wheat (*Triticum monococcum* L.) accessions from Europe, North Africa and Near East indicated that there were two main gene pools, one was from Morocco and the Iberian Peninsula and the other was from Europe and Near East in einkorn. Gene diversity ranged between $H = 0.411$ in Iberia Peninsula and $H = 0.594$ in other einkorn accessions (Oliveira et al. 2011).

Heun et al. (1997) investigated the origin of domestication site of *T. monococcum* using molecular markers (AFLP). The molecular data suggested that a wild group of *Triticum monococcum* ssp. *boeoticum* lines from the Karacadağ mountains (southeast Turkey) was the likely progenitor of cultivated einkorn varieties along with the evidence from archaeological excavations of early agricultural settlements near the Karacadağ mountains, where domestication of einkorn wheat began.

The wild einkorn underwent a process of natural genetic differentiation, most likely an incipient speciation, and prior to domestication. It was determined that three genetically, and to some extent morphologically, distinct wild einkorn races existed, and they were designed as a, b and c. Race b was used by humans for domestication (Kilian et al. 2007). The observations of higher genetic diversity in domesticated einkorn are inferring that domestication process had no effect on the reduction of genetic diversity in einkorn wheat. A specific wild einkorn race that arose without human intervention was subjected to multiple independent domestication events (Kilian et al. 2007).

The genetic diversity analyses in einkorn wheat (*Triticum urartu*, *T. boeoticum* and T. *monococcum*) and *Aegilops* ssp. (*Ae. speltoides* and *Ae. squarrosa*) in terms of DNA markers (AFLP and SSLP) clearly indicated that *T. urartu* was greatly differentiated from the other two A genome species. The observations of less intraspecific DNA variations of the nuclear genomes within the einkorn wheat ssp. were consistent with Kilian et al. (2007) and were smaller than those within the two *Aegilops* species that displayed the largest nuclear genome variation, while its chloroplast genome variation was the least (Mizumoto et al. 2002).

The analysis of the germplasm of Iranian einkorn group (*T. monococcum*, *T. boeoticum* subsp. *boeoticum*, *T. boeoticum* subsp. *thaoudar* and *T. urartu*) using DNA markers (IRAP) produced great polymorphism, 84% of which was attributed to total variation within population and the remaining 16% was among the species according to AMOVA (Farouji et al. 2015). The close genetic similarity among the species revealed the high affinity, gene flow and genetic relationships between species belonging to einkorn. The genetic distance value was high between *T. monococcum* and *T. urartu* and low between *T. boeoticum* subsp. *boeoticum* and *T. boeoticum* subsp. *thaoudar*. A centre of high diversity in the west and the northwest of Iran clearly exposed patterns of two distinct geographic regions (Farouji et al. 2015). Microsatellite markers (SSRs) are a very powerful new tool to support the determination of critical races in diploid wild wheat species (Hammer et al. 2000).

4.5.2 *Emmer Wheat (*Triticum turgidum *ssp.* dicoccon *Schrank Tell.) Landraces*

Turkey is the country where emmer wheat originated and travelled through the Balkans, Italy, Spain and the North African countries. The Gene Bank material of emmer wheat (*Triticum turgidum* L. ssp. *dicoccon* (Schrank) Thell.) germplasm conserved in Aegean Agricultural Research Institute in Izmir, Turkey, was analysed to determine genetic diversity in terms of DNA markers (SSRs), which produced 100% polymorphic 497 alleles and displayed great genetic variation ($H_e = 0.9$). The genetic differentiation was between 15% and 85% within populations. Landraces displayed higher genetic diversity estimates for the *A* genome than the *B* genome, while the SSR loci at telomeric and sub-telomeric regions displayed lower genetic diversity than other regions on the chromosomes. x-gwm-312, a microsatellite marker reported having linkage with the salinity tolerance in wheat, displayed the highest polymorphism ($H_e = 0.97$) among the SSR markers used for analysis. Thus, Turkish emmer wheat germplasm conserved in the Gene Bank might have potential salinity tolerance that could be exploitable in formal wheat breeding programmes (Özbek and Demir 2019).

The molecular analysis of emmer wheat (*Triticum dicoccon* Schrank Thell.) accessions from India including 28 from a local collection and 20 Indian accessions obtained from CIMMYT, Mexico, using DNA markers (SSR) indicated that emmer wheat accessions had a high level of similarity, and Indian emmer wheats were not very diverse. The breeders could exploit the diversity from other ecogeographic groups or even from other wheat species to increase the diversity within the Indian emmer wheat ecogeographic group (Salunkhe et al. 2013).

Ethiopian tetraploid wheat landraces consisting of three species *Triticum durum* Desf., *T. dicoccon* Schrank and *T. turgidum* L. displayed a high level of polymorphism and a large number of alleles unique for each species based on microsatellite marker analysis. A higher genetic diversity was observed in *T. durum* compared to emmer (*T. dicoccon*) and popular (*T. turgidum*) wheats. This might be related with Ethiopia as one of the places, where durum wheat landrace cultivation is carried out in wide areas. The A genome was more polymorphic than the B genome in all the three species. Genetic distances were lower between *T. durum* and *T. turgidum* than between *T. durum* and *T. dicoccon* or between *T. turgidum* and *T. dicoccon* (Teklu et al. 2006).

*4.5.3 Durum Wheat (***Triticum turgidum** *var.* **durum** *Desf.) Landraces*

The molecular analysis of Turkish durum wheat landraces by means of RAPD markers indicated that the landraces had high level of genetic diversity estimates for observed heterozygosity and gene diversity. Some morphological traits (plant height, spike length, grain number per spike, biological yield, resistance to lodging, etc.), pathological traits (stripe and leaf rusts) and technological traits (1000-kernel weight, hectolitre weight, protein ratio, SDS sedimentation, etc.) were also investigated along with RAPD markers and showed great variation. Altogether, these results display that Turkish durum wheat landraces have great genetic diversity not only for expected genetic diversity but also for observed genetic diversity along with variation in other characteristics, that is, exploitable in breeding programmes of development of commercial cultivars, which have lower genetic diversity than landraces in the present study, with higher yield, resistance to rusts and desirable quality traits (Akar and Ozgen 2007).

Greek landraces and cultivars of durum wheat (*Triticum turgidum* L. var. *durum* (Desf.)), commercial bread wheat (*Triticum aestivum* L.) cultivars and a genotype of *Triticum monococcum* L. were assessed in terms of DNA markers (RAPD) and produced great polymorphism, 125 polymorphic fragment (83.3%). The overall results indicated that durum wheat landraces were sharing some fragments with bread, while *T. monococcum* was standing apart from all other genotypes (Mantzavinou et al. 2005).

*4.5.4 Bread Wheat (*Triticum aestivum *L.) Landraces*

Characterisation of genetic diversity based on molecular data in different plant species is the recent advancement to gain knowledge about genetic structure of natural or cultivated plant species nowadays. This is an important issue for explaining the phylogenetic relationships among the plant species particularly closely related species, to understand their evolutionary dynamics and to predict their future tendencies, to investigate origin of species, to explore the amount of genetic diversity in wild and primitive relatives of modern crop plant varieties and to exploit their germplasm, which have substantially high genetic diversity and harbouring different gene combinations for the biotic and abiotic stress factors, for improvement of high yielding commercial cultivars adaptable to specific environmental conditions. It was proved that some molecular markers are associated with some desired genes, which are concerned in quality, yield or resistance to the biotic and abiotic stress factors. Recent advances in molecular marker technology enabled the scientists to access the data stored in the gold mine of DNA in the organisms. The molecular markers have been used in different modern wheat species and varieties as well as in wild and primitive wheat species for several decades.

The hexaploid wheat (*Triticum aestivum* L.) landrace collection covering most of the cultivation areas in northern Oman had high genetic diversity. Omani wheat landraces from different districts showed that they have different allele combinations, which was revealed by the correlation values between genetic diversity and allele number. Omani wheat landraces had well adaptation in different environmental conditions and maintains the high level genetic diversity (Al Khanjari et al. 2007)..

The characterisation of genetic diversity in a collection of wheat landraces, whichwere collected from different regions of Turkey based on the data obtained from the analysis of microsatellite markers and some morphological traits, indicated that Turkish wheat landraces have been grouped into two distinct groups according to genotypes and phenotypes based on microsatellite markers and morphological traits, respectively. In both cases, Turkish wheat landraces displayed great variation (Sönmezoğlu et al. 2012).

Afghanistan has important agroecological zones as a secondary origin of wheat for investigation of the genetic diversity and novel alleles/allele combinations. A wheat landrace collection (400) of Dr. Hitoshi Kihara et al. was screened by using diversity array technology and single-nucleotide polymorphism markers, as well as diagnostic molecular markers at important loci controlling vernalisation (*Vrn*), photoperiod response (*Ppd*), grain colour (*R*), leaf rust (*Lr*), yellow rust (*Yr*), stem rust (*Sr*) and Fusarium head blight (*Fhb*). The results indicated that Afghanistan wheat landrace collection had 53% winter types, 43% either spring types or facultative types and 4% either unknown or had *Vrn-A1c*, which is a rare spring allele;

nevertheless, confirmation is needed with additional genotyping and phenotyping, and 97% of the lines represented a photosensitive allele for photoperiod response. For the characterisation of grain colour, 39% of landraces displayed white grain, and 17 unique landraces were determined as resistant to rust and *Fhb* (Manickavelu et al. 2014).

Omani durum wheat (*Triticum durum* Desf.) and bread wheat (*Triticum aestivum* L.) landraces displayed that the genetic diversity was conserved within populations rather than between. The durum wheat landraces displayed the higher genetic diversity than bread wheat landraces that might be due to their different domestication history. Omani bread wheat landraces were resembling Turkish and Mexican bread wheat landraces as reported in the previous studies. There was no close relation between Omani bread wheat landraces and today's landraces from Africa, Asia, Western Europe, Turkey and Central or South America. According to the cluster analysis, Omani bread wheat landraces clustered together with two landraces from Pakistan that might be a possible, previously unknown relationship (Zhang et al. 2006).

Using a SNP-based diversity map, Cavanagh et al. (2013) characterised the impact of crop improvement on the genomic and geographic patterns of the genetic diversity. Their results suggested that loci targeted by selection for wheat improvement have changed over time, potentially reflecting the breeding efforts aimed at developing higher yielding varieties that are adapted to the new or changing local conditions.

Next-generation sequencing (NGS) technologies will still open new undiscovered possibility for analysis of the genetic and management of genetic diversity and more precise, rapid and successful utilisation for wheat improvement.

References

Akar T, Ozgen M (2007) Genetic diversity in Turkish durum wheat landraces. In: Buck HT, Nisi JE, Salomón N (eds) Wheat production in stressed environments. Developments in plant breeding, vol 12. Springer, Dordrecht

Al Khanjari S, Filatenko AA, Hammer K, Buerkert A (2008) Morphological spike diversity of Omani wheat. Genet Resour Crop Evol 55(8):1185–1195

Al Khanjari S, Hammer K, Buerkert A, Röder MS (2007) Molecular diversity of Omani wheat revealed by microsatellites: II. Hexaploid landraces. Genet Resour Crop Evol 54(7):1407–1417

Alsaleh A, Baloch FS, Nachit M, Ozkan H (2016) Phenotypic and genotypic intra-diversity among Anatolian durum wheat "Kunduru" landraces. Biochem Syst Ecol 65:9–16

Alvarez JB, Caballero L, Ureña P, Vacas M, Martín LM (2007) Characterisation and variation of morphological traits and storage proteins in Spanish emmer wheat germplasm (*Triticum dicoccon*). Genet Resour Crop Evol 54(2):241–248

Alvarez JB, Moral A, Martín LM (2006) Polymorphism and genetic diversity for the seed storage proteins in Spanish cultivated einkorn wheat (*Triticum monococcum* L. ssp. *monococcum*). Genet Resour Crop Evol 53:1061–1067

Al-Ajlouni MM, Jaradat AA (1997) Diversity in durum wheat landraces collected from Jordan I. Quantitative Traits. Cereal Res Commun 25(2):169–175

Asins MJ, Carbonell EA (1989) Distribution of genetic variability in a durum wheat world collection. Theor Appl Genet 77:287–294

Bechere E, Belay G, Mitiku D, Merker A (1996) Phenotypic diversity of tetraploid wheat landraces from northern and north-central regions of Ethiopia. Hereditas 124:165–172

Belay G, Bechere E, Mitiku D, Merker A, Tsegaye S (1997) Patterns of morphological diversity in tetraploid wheat (*Triticum turgidum* L.) landraces from Ethiopia. J Acta Agric Scandinavica, Section B– Soil Plant Science 47(4):221–228

Belay G, Furuta Y (2001) Zymogram patterns of α-amylase isozymes in Ethiopian tetraploid wheat landraces: insight into their evolutionary history and evidence for gene flow. Genet Resour Crop Evol 48:507–512

Bradshaw AD (1965) Evolutionary significance of phenotypic plasticity in plants. Adv Genet 13:115–155

Buerkert A, Oryakhail M, Filatenko AA, Hammer K (2006) Cultivation and taxonomic classification of wheat landraces in the Upper Panjsher Valley of Afghanistan after 23 years of war. Genet Resour Crop Evol 53(1):91–97

Butnaru G, Sarac I, Blidar A, Holly L, Mar I (2003) Morpho-agronomic variability of *Triticum monococcum* L. landraces in the Timisoara area. ISIRR, Section IV, Hunedoara, Romania, p 167

Cavanagh C, Chao S, Wang S et al (2013) Genome-wide comparative diversity uncovers multiple targets of selection for improvement in a worldwide sample of hexaploid wheat landrace and cultivars. Proc Natl Acad Sci U S A 110(20):8057–8062. www.pnas.org/cgi/doi/10.1073/pnas.1217133110

Ciaffi M, Benedettelli S, Giorgi B, Porceddu E, Lafiandra D (1991) Seed storage proteins of *Triticum turgidum* ssp. *dicoccoides* and their effect on the technological quality in durum wheat. Plant Breed 107:309–319

Ciaffi M, Dominici L, Lafiandra D, Porceddu E (1992) Seed storage proteins of wild wheat progenitors and their relationships with technological properties. Hereditas 116:315–322

Ciaffi M, Lafiandra D, Porceddu E, Benedettelli S (1993) Storage-protein in wild emmer (*Triticum turgidum* ssp. *dicoccoides*) from Jordan and Turkey. II. Patterns of allele distribution. Theor Appl Genet 86:518–525

Ciaffi M, Dominici L, Lafiandra D (1997) Gliadin polymorphism in wild and cultivated einkorn wheats. Theor Appl Genet 94:68–74

Corazza L, Pasquini M, Perrino P (1986) Resistance to rusts and powdery mildew in some strains of *Triticum monococcum* L. and *Triticum dicoccum* Schubler cultivated in Italy. Genetica Agraria 40:243–254

Damania AB, Hakim S, Moualla MY (1992) Evaluation of variation in *Triticum dicoccum* for wheat improvement in stress environment. Hereditas 116:163–166

Damania AB, Srivastrava JP (1990) Genetic resources for optimal input technology ICARDA's perspectives. In: El-Bassam N, Dambrot M, Loughman BC (eds) Genetic aspects of plant mineral nutrition. Kluwer, Dordrecht, The Netherlands, pp 425–430

Desheva G (2014) Morphological and agronomical characterization of common wheat landraces (*Triticum aestivum* L.) from the National Wheat Collection of Bulgaria. Emir J Food Agric 26(2):164–169

D'Antuono LF, Minelli M (1998) Yield and yield components analysis of emmer wheat (*Triticum dicoccum* Schubler) landraces from Italy. In: Jaradat AA (ed) Proceedings of the 3rd international Triticeae symposium, May 1997, Aleppo Syria. Science Publisher Inc, USA, pp 393–404

Elings A, Nachit MM (1991) Durum wheat landraces from Syria. I Agro-ecological and morphological characterization. Euphytica 53(3):211–224

Eticha F, Belay G, Bekele E (2006) Species diversity in wheat landrace populations from two regions of Ethiopia. Genet Resour Crop Evol 53(2):387–393

Farouji E, Khodayari A, Saeidi H et al (2015) Genetic diversity of diploid Triticum species in Iran assessed using inter-retroelement amplified polymorphisms (IRAP) markers. Biologia 70:52–60

Galterio G, Codianni P, Novembre G, Saponaro C, Di Fonzo N, Pogna NE (1998) Storage protein composition and technological characteristics of F6 lines from the cross *Triticum turgidum* spp. *durum* × *Triticum turgidum* spp. *dicoccum*. In: Proceedings of the 9th international wheat genetics symposium, vol 4, Saskatoon, Canada, pp 148–150

Ghimire SK, Akashi Y, Maitani C, Nakanishi M, Kato K (2005) Genetic diversity and geographical differentiation in Asian common wheat (*Triticum aestivum* L.), revealed by the analysis of peroxidase and esterase isozymes. Breed Sci 55(2):175–185

Hammer K, Filatenko AA, Korzun V (2000) Microsatellite markers – a new tool for distinguishing diploid wheat species. Genet Resour Crop Evol 47:497–505

Heun M, Schäfer-Pregl R, Klawan D, Castagna R, Accerbi M, Borghi B, Salamini F (1997) Site of einkorn wheat domestication identified by DNA finger printing. Science 278:1312–1314

Jakubziner MM (1969) Immunity of different wheat species. Agric Biol 4:837–847. (in Russian)

Jaradat AA (2013) Wheat landraces: a mini review. Emir J Food Agric 25(1):20–29

Jaradat AA (1991) Phenotypic divergence for morphological and yield-related traits among landrace genotypes of durum wheat from Jordan. Euphytica 52(3):155–164

Jaradat AA (2014) The vanishing wheat landraces of the Fertile Crescent. Emir J Food Agric 26(2):203–217

Kamali MRJ, Bozorghipour R, Moghaddam ME, Kamali MRJ, Kazemi S, Amini A, Bozorgipour R, Najafian G, Baghaei N (2011) Assessment of high molecular weight glutenin sub-units and baking quality related traits in some of the Iranian bread wheat (*Triticum aestivum* L.) landraces. Crop Breed J 1(1):29–40

Keskin SŞ, Özbek Ö, Eser V, Taşkin Göçmen B (2015) Polymorphism in seed endosperm proteins (gliadins and Glutenins) of Turkish cultivated einkorn wheat [*Triticum monococcum* ssp. *monococcum*] landraces. Cereal Res Commun 43(1):108–122

Kilian B, Özkan H, Walther A, Kohl J, Dagan T, Salamini F, Martin W (2007) Molecular diversity at 18 loci in 321 wild and 92 domesticate lines reveal no reduction of nucleotide diversity during *Triticum monococcum* (einkorn) domestication: implications for the origin of agriculture. Mol Biol Evol 24:2657–2668

Kimber G, Feldman M (1987) Wild wheats: an introduction. Special Report 353. College of Agriculture, Columbia, Missouri, pp. 1–142

Mantzavinou A, Bebeli PJ, Kaltsikes PJ (2005) Estimating genetic diversity in Greek durum wheat landraces with RAPD markers. Aust J Agric Res 56:1355–1364

Manickavelu A, Niwa S, Ayumi K, Komatsu K, Naruoka Y, Ban T (2014) Molecular evaluation of Afghan wheat landraces. Plant Genet Res 12(1):31–35

Mac Key J (1966) Species relationship in *Triticum*, Proc. of 2nd Int. Wheat Genetics Symp. Hereditas 2:237–276

Mizumoto K, Hirosawa S, Nakamura C, Takumi S (2002) Nuclear and chloroplast genome genetic diversity in the wild einkorn wheat, *Triticum urartu*, revealed by AFLP and SSLP analyses. Hereditas 137:208–214

Moghaddam M, Ehdaie B, Waines JG (1997) Genetic variation and interrelationships of agronomic characters in landraces of bread wheat from southeastern Iran. Euphytica 95(3):361–369

Motalebi M, Keshavarzi M, Naghavi MR (2007) Glutenin subunit composition in durum (*Triticum durum*) landraces and cultivars. Asian J Plant Sci 6:399–402

Naghavi MR, Monfared SR, Ahkami AH, Ombidbakhsh MA (2009) Genetic variation of durum wheat landraces and cultivars using morphological and protein markers. World Acad Sci Eng Technol 25:73–75

Nicotra AB, Atkin OK, Bonser SP et al (2010) Plant phenotypic plasticity in a changing climate. Trends Plant Sci 15:684–692

Oliveira HR, Jones H, Leigh F et al (2011) Phylogeography of einkorn landraces in the Mediterranean basin and Central Europe: population structure and cultivation history. Archaeol Anthropol Sci 3:327

Oliveira HR, Campana MG, Jones H, Hunt HV, Leigh F, Redhouse DI, Lister DL, Jones MK (2012) Tetraploid wheat landraces in the Mediterranean Basin: taxonomy, evolution and genetic diversity. PLoS One 7(5):e37063

Oliver RE, Cai X, Friesen TL, Halley S, Stack RW, Xu SS (2008) Evaluation of Fusarium head blight resistance in tetraploid wheat (*Triticum turgidum* L.). Crop Sci 48:213–222

Özbek Ö, Taskin BG, Şan SK, Eser V, Arslan O (2011) Gliadin polymorphism in Turkish cultivated emmer wheat (*Triticum turgidum* L. ssp. *dicoccon* (Schrank) Thell.) landraces. Plant Syst Evol 296(1–2):121–135

Özbek Ö, Taşkın BG, Şan SK, Eser V, Arslan O (2012) High-molecular-weight glutenin subunit variation in Turkish emmer wheat [*Triticum turgidum* L. ssp. *dicoccon* (Schrank) Thell.] landraces. Plant Syst Evol 298:1795–1804

Özbek Ö, Taskin BG, Şan SK, Eser V, Arslan O (2013) Genetic characterization of Turkish cultivated emmer wheat [*Triticum turgidum* L. ssp. *dicoccon* (Schrank) Thell.] landraces based on isoenzyme analysis. Cereal Res Commun 41(2):304–315

Özbek Ö, Demir S (2019) Characterization of genetic diversity in cultivated emmer wheat [*Triticum turgidum* L. ssp. *dicoccon* (Schrank) Thell.] landrace populations from Turkey by SSR. Russ J Genet 55:969–977

Özkan H, Brandolini A, Schafer-Pregl R, Salamini F (2002) AFLP analysis of a collection of tetraploid wheats indicates the origin of emmer and hard wheat domestication in Southeast Turkey. Mol Biol Evol 19:1797–1801

Özkan H, Brandolini A, Pozzi C et al (2005) A reconsideration of the domestication geography of tetraploid wheats. Theor Appl Genet 110:1052–1060

Pagnotta MA, Mondini L, Atallah MF (2005) Morphological and molecular characterization of Italian emmer wheat accessions. Euphytica 146(1–2):29–37

Payne PI, Lawrence GJ (1983) Catalogue of alleles for the complex gene loci, *Glu-A1*, *Glu-B1*, and *Glu-D1*, which code for high molecular weight subunits of glutenin in hexaploid wheat. Cereal Res Commun 11:29–35

Payne PI, Corfield KG (1979) Subunit composition of wheat glutenin proteins, isolated by gel filtration in a dissociating medium. Planta 145:83–88

Piergiovanni AR, Laghetti G, Perrino P (1996) Characteristics of meal from hulled wheats (*Triticum dicoccum* Schübler and *Triticum spelta* L.): an evaluation of selected accession. Cereal Chem 73(6):732–735

Salinas J, Vega MP, Benito C (1982) Identification of hexaploid wheat cultivars based on isozyme patterns. J Sci Food Agric 33(3):221–226

Salunkhe A, Tamhankar S, Tetali S, Zaharieva M, Bonnett D, Trethowan R, Misra S (2013) Molecular genetic diversity analysis in emmer wheat (*Triticum dicoccon* Schrank) from India. Genet Resour Crop Evol 60:165–174

Sönmezoğlu ÖA, Bozmaz B, Yildirim A, Kandemir N, Aydin N (2012) Genetic characterization of Turkish bread wheat landraces based on microsatellite markers and morphological characters. Turk J Biol 36:589–597

Stallknecht GF, Gilbertson KM, Ranney JE (1996) Alternative wheat cereals as food grains: einkorn, emmer, spelt, kamut, and triticale. In: Janick J (ed) Progress in new crops. ASHS Press, Alexandria, VA, pp 156–170

Teklu Y, Hammer K, Huang X et al (2006) Analysis of microsatellite diversity in Ethiopian tetraploid wheat landraces. Genet Resour Crop Evol 53:1115–1126

Terasawa Y, Kawahara T, Sasakuma T, Sasanuma T (2009) Evaluation of the genetic diversity of an Afghan wheat collection based on morphological variation, HMW glutenin subunit polymorphisms, and AFLP. Breed Sci 59(4):361–371

Tesfaye T, Getachew B, Worede M (1991) Morphological diversity in tetraploid wheat landrace populations from the central highlands of Ethiopia. Hereditas 114:171–176

Teshome A, Baum BR, Fahrig L, Torrance JK, Arnason TJ, Lambert JD (1997) Sorghum (*Sorghum bicolor* (L.) Moench) landrace variation and classification in North Shewa and South Welo, Ethiopia. Euphytica 97:255–263

Tsegaye S, Tesemma T, Belay G (1996) Relationships among tetraploid wheat (*Triticum turgidum* L.) landrace populations revealed by isozyme markers and agronomic traits. Theor Appl Genet 93:600–605

Turcotte MM, Levine JM (2016) Phenotypic plasticity and species coexistence. Trends Ecol Evol 31(10):803–813

Uzundzalieva K, Desheva G, Valchinova E, Kyosev B (2016) Comparative evaluation of einkorn accessions (*Triticum monococcum* L.) of some main agricultural characters. Agron J 17(1):69–80

Zeven AC (1998) Landraces: a review of definitions and classifications. Euphytica 104:127–139

Zeven AC (1999) The traditional inexplicable replacement of seed and seed ware of landraces and cultivars: a review. Euphytica 110:181–191

Zhang P, Dreisigacker S, Buerkert A, Alkhanjari S, Melchinger AE, Warburton ML (2006) Genetic diversity and relationships of wheat landraces from Oman investigated with SSR markers. Genet Resour Crop Evol 53(7):1351–1360

Zuli Y et al (1999) The study on esterase and peroxidase isozymes in landraces of wheat from to Sichuan. Journal of Sichuan Agricultural University. http://en.cnki.com.cn/Journal_en/D--D000-SCND-1999-04.htm

Getachew B, Tesemma T., Becker HC, Merker A (1993) Variation and interrelationships of agronomic traits in Ethiopian tetraploid wheat landraces. Euphytica 71(3): 181–188