Genetic Diversity, Evolution and Domestication of Wheat and Barley in the Fertile Crescent

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Abstract About 12,000 years ago, humans began the transition from hunter-gathering to a sedentary, agriculture-based society. From its origins in the Fertile Crescent, farming expanded throughout Europe, Asia and Africa, together with various domesticated plants and animals. Where, how and why agriculture originated is still debated. Progress has been made in understanding plant domestication in the last few years. The approach to understanding cereal domestication that we have taken in recent years has, in the main, involved the following five-pronged strategy: (1) the use of comprehensive germplasm collections covering the whole distribution area for each species and the collection of new germplasm for wild cereals from their primary habitats in nature; (2) the comparison of many wild and domesticated accessions for each species; (3) the identification of the wild progenitor in the wild gene pool and via comparison of genetic similarity across many loci with domesticate descendants; (4) the use of molecular fingerprinting techniques at

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many loci to compare wild and domesticate cereals; (5) the identification and cloning of genes involved in domestication. That work has provided some insights into the domestication process, insights that, placed in the archaeological context of human history in the Fertile Crescent, provide information about what humans were doing while domestication was taking place. This chapter reviews recent developments in our understanding of wheat and barley domestication history in the Fertile Crescent, events that forged the foundations of our present-day European culture.

During SPP 1127: Scope of this Study.

The main aim of the study during SPP1127 was to investigate and compare nucleotide diversity between wild and domesticated wheat and barley using large germplasm collections and different molecular markers to obtain new insights and to contribute to the ongoing discussion on the origin of agriculture and plant domestication in the Fertile Crescent.

Keywords Genetic diversity · Evolution · Domestication · Wheat · Barley · Fertile Crescent

1 Introduction

Cereals provide more than 50% of the worldwide crop production and are important renewable resources for food, feed, and industrial materials (http://faostat.fao.org). The Triticeae tribe within the Pooideae subfamily of the grass family Poaceae includes the crop genera *Triticum* (wheat), *Hordeum* (barley) and *Secale* (rye). Wheat is the primary cereal of temperate regions and the staple food for about 40% of the world's population. Globally, wheat is the second most widely grown crop, just recently superseded by maize, while barley ranks fourth after maize, wheat and rice (http://faostat.fao.org). Wheat and barley are the most important staple crops of Europe and of the western part of Asia. Wheat is mainly used for bread (*Triticum aestivum*, hexaploid) and pasta (*Triticum durum*, tetraploid), barley as fodder and for brewing beer, while rye is used for bread and fodder. Human history is closely interwoven with these three staple crops, because wheat and barley (and possibly also rye) belong to the Neolithic founder crops upon which western agriculture was built.

2 Origins of Cultivated Plants and Agriculture: A Brief Historical Overview

The origin of cultivated plants and their domestication have been of relevant interest beginning with the essays of Alexander von Humboldt (*Essai sur la géographie des plantes*, Humboldt von 1806; Fiedler and Leitner 2000), Charles

Darwin (*The origin of species*, Darwin 1859 and *The variation of animals and plants under domestication*, Darwin 1868), and Alphonse de Candolle (*Origine de plantes cultivées*, Candolle de 1883; Damania 1998).

In 1926, Nikolay Ivanovich Vavilov published his book *Centers of origin of cultivated plants* (Vavilov 1926). Vavilov noted that "the entire varietal and racial diversity of the field and vegetable crops is concentrated in mountainous districts". Vavilov summarized all his work on diversity in 1935 in *The phytogeographical basis for plant breeding* in which he describes eight centers, including a Mediterranean Center where wheats, barleys, vegetables and fruits originated (Vavilov 1992; Hawkes 1998). Two years later, the archaeologist and philosopher Vere Gordon Childe presented his "Oasis Theory" which proposed that agriculture began in the Near East when the climate changed at the end of the last glacial period, a process that he termed "Neolithic Revolution" (Childe 1928, 1936; Harris 1998). Subsequent work by Robert Braidwood who excavated Jarmo (Braidwood and Braidwood 1950) and Cayönü (Braidwood et al. 1969) led to the suggestion that agriculture began in the "hilly flanks of Breasted's 'Fertile Crescent'" (Braidwood and Braidwood 1950; Braidwood 1972; Braidwood, et al. 1983). The term "Fertile Crescent" (Fig. 1) stems in turn from James Henry Breasted (Breasted 1938; Braidwood 1972). Archaeological evidence, however, only tells part of the story about domestication, and contributions from (archaeo-) botany and genetics have significantly enriched our understanding of agriculture origins (Harlan and Zohary 1966; Harlan 1971, 1975, 1995; Hillman and Davies 1990; Nesbitt 1995, 2002; Nesbitt and Samuel 1996; Willcox 1996, 2005; Zohary 1999; Hillman 2000; Tanno and Willcox 2006).

For more than two decades, the use of molecular markers has been providing new information on genetic diversity of crop plants in relation to wild relatives, centers of domestication, time frame of the domestication process, and specific

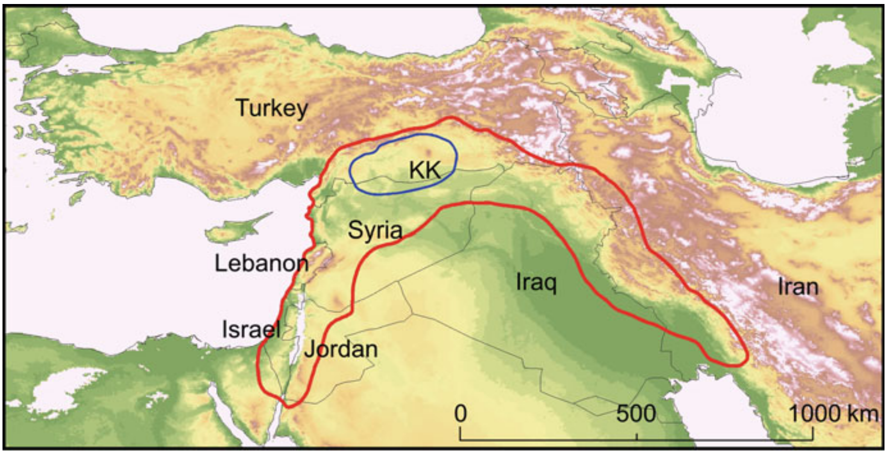

Fig. 1 Fertile Crescent and "core area" of plant domestication within the Fertile Crescent. The Fertile Crescent is indicated with a *red line* and the "core area" is shown with a *blue line*. *KK* Karacadag mountain range in south-eastern Turkey

alleles supporting domesticated traits. The connection between molecular markers and domestication geography took root in the paper by Heun et al. (1997), who found that, on the basis of AFLP (amplified fragment length polymorphism) markers, the closest wild relatives of domesticated einkorn (*Triticum monococcum*, diploid) occur in a very restricted area within the Karacadag mountain range in south-eastern Turkey (Fig. 1). From that, they concluded, not unreasonably, that this represents the site where humans first domesticated einkorn. Important contributions using different molecular markers for other species followed: barley (Badr, et al. 2000; Kilian et al. 2006; Morrell and Clegg 2007); einkorn (Kilian et al. 2007b); emmer (Ozkan et al. 2002, 2005; Mori et al. 2003; Luo et al. 2007); maize (Wright et al. 2005); rice (Londo et al. 2006), and sorghum (Hamblin et al. 2006).

3 Evolution and Domestication of *Triticeae*

Archaeological evidence documents the occurrence of plant remains at different excavation sites, in different stratigraphic layers that were analyzed and radiocarbon dated (Hillman 2000), from which a generally consistent picture emerges indicating that western agriculture originated in the Fertile Crescent after the last ice age, in aceramic Pre-Pottery Neolithic (PPN) from about 12,000 to 9,500 years ago (Zohary and Hopf 2000; Nesbitt 2002; Salamini et al. 2002). It is now widely held that Fertile Crescent agriculture originated in a "core area" in south-eastern Turkey to northern Syria (Fig. 1), where the distribution of wild forms (Fig. 2) are molecularly and cytologically closely related to the founder crops (Table 1) (Lev-Yadun et al. 2000; Abbo et al. 2006). From there, farming spread throughout

Fig. 2 Wild einkorn, wild emmer and *Aegilops* species in their natural habitat within the Karacadag mountain range. Picture taken by H. Özkan in early July 2004

Table 1 The founder crops of Neolithic agriculture and their wild progenitors

Name	Wild progenitor	Domesticated form
Einkorn wheat[a]	*Triticum boeoticum*	*T. monococcum*
Emmer wheat[b]	*Triticum dicoccoides*	*T. dicoccon*
Rye	*Secale vavilovii*	*S. cereale*
Barley	*Hordeum spontaneum*	*H. vulgare*
Lentil	*Lens orientalis*	*L. culinaris*
Pea	*Pisum humile*	*P. sativum*
Chickpea	*Cicer reticulatum*	*C. arietinum*
Bitter vetch	*Vicia ervilia*	*V. ervilia*
Flax	*Linum bienne*	*L. usitatissimum*

[a]It is still unclear if *Triticum urartu* was also collected, due to the fact that seeds of *T. urartu* and *T. boeoticum* cannot be distinguished

[b]Evidence supports that wild *Triticum araraticum* was the progenitor of *T. timopheevii,* but distinguishing plant remains of wild *T. dicoccoides* from those of wild *T. araraticum*, as well the two domesticates, is almost impossible

Europe, Asia and Africa (Ammerman and Cavalli-Sforza 1984; Nesbitt 2002). The domestication process lasted several centuries in the region (Tanno and Willcox 2006), always preceded by cultivation of wild populations before domestication (Weiss et al. 2006; Willcox et al. 2008).

Wild relatives differ from their crop descendants (Table 1) in several phenotypic characteristics (Fig. 3), collectively referred to as the "domestication syndrome" (Hammer 1984; Salamini et al. 2002; Kilian et al. 2009). The most important *Triticeae* traits modified during domestication were the free-threshing state and brittle rachis. Free threshing means that the seeds are released from the rachis at threshing, and brittle rachis means that the dried inflorescence (head) does not disarticulate at maturity (Fig. 3). Additional modifications taking place during domestication and subsequent breeding concerned seed size (larger seeds in domesticate forms), kernel row type (more rows in some domesticated species), plant height, grain hardness, tillering, seed dormancy, photoperiod, vernalization, and heading date. In addition, the spread of the domesticated cereals out of the Fertile Crescent required the adaptation to new environments supported by newly arisen favorable alleles at critical genetic loci (for more information, see Salamini et al. 2002; Kilian et al. 2009).

Wild and domesticated cereals are often designated as separate species, although this is as much for convenience sake, because their crossing progenies are usually fertile. However, it is common to refer to them, at least when describing archaeological and genetical events, as if they are different species, a formality which simplifies the discussion of domestication-related issues. Over the years, taxonomical classifications were developed by geneticists. For wheat, the latest comprehensive, systematic overview was completed in 1979 by Dorofeev and colleagues. In this chapter, the nomenclature and the genome formula given for *Triticum* by Dorofeev et al. (1979) and the *Aegilops* nomenclature based on van Slageren (1994) is mainly followed. In general, the Zohary and Hopf (2000) classification is accepted, with a few modifications where necessary (Table 2).

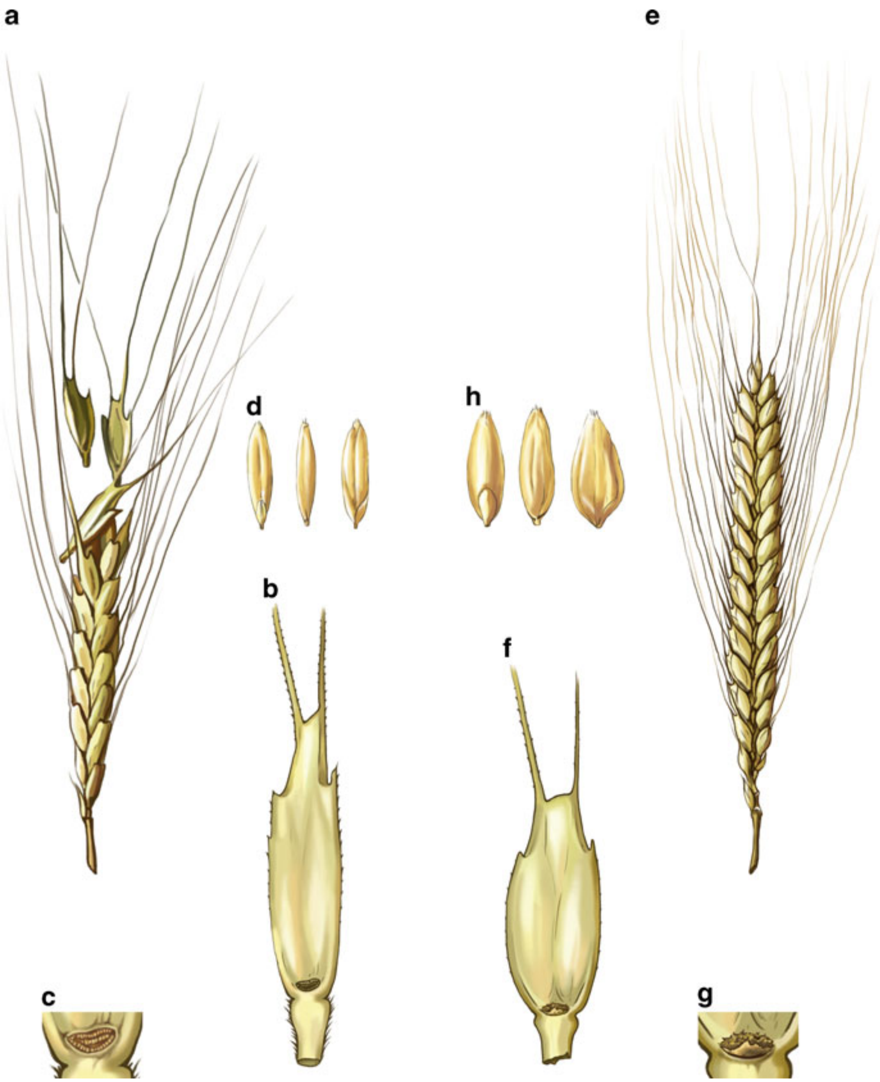

Fig. 3 Morphological differences between wild and domesticated einkorn wheat. Examples of dehiscent wild einkorn wheat ear (**a**), wild einkorn spikelet (**b**), detail of wild einkorn spikelet with smooth wild abscission scar (**c**) and wild einkorn seeds (**d**). Indehiscent domesticated ear (**e**), domesticated spikelet (**f**), detail of domesticated spikelet with jagged break (**g**) and domesticated seeds (**h**). This figure was kindly prepared by S. Kilian

Archaeological evidence indicates that plant remains of nine domesticated species very often appear together at common sites and times. It is therefore assumed that these species have been domesticated together as a "founder package" (Lev-Yadun et al. 2000). The wild and domesticated species of the Neolithic founder package are shown in Table 1.

Table 2 Comparative classification table for *Triticum* (modified from http://www.k-state.edu./wgrc). The traditional genome formulas are included

Genome	Dorofeev et al. (1979)	Mac Key (1988)	van Slageren (1994)	Kimber and Sears (1987)
A^u	*T. urartu*	*T. urartu*	*T. urartu*	*T. monococcum*
A^b	*T. boeoticum*	*T. monococcum* ssp. *boeoticum*	*T. monococcum* ssp. *aegilopoides*	*T. monococcum*
A^b	*T. monococcum*	*T. monococcum* ssp. *monococcum*	*T. monococcum* ssp. *monococcum*	*T. monococcum*
A^b	*T. sinskajae*			
AB	*T. aethiopicum*			
AB	*T. carthlicum*	*T. turgidum* ssp. *carthlicum*	*T. turgidum* ssp. *carthlicum*	*T. turgidum*
AB	*T. dicoccoides*	*T. turgidum* ssp. *dicoccoides*	*T. turgidum* ssp. *dicoccoides*	*T. turgidum*
AB	*T. dicoccon*	*T. turgidum* ssp. *dicoccum*	*T. turgidum* ssp. *dicoccum*	*T. turgidum*
AB	*T. durum*	*T. turgidum* ssp. *turgidum* conv. *durum*	*T. turgidum* ssp. *durum*	*T. turgidum*
AB	*T. ispahanicum*			
AB	*T. jakubzineri*			
AB	*T. karamyschevii*	*T. turgidum* ssp. *georgicum*	*T. turgidum* ssp. *paleocolchicum*	
AB	*T. polonicum*	*T. turgidum* ssp. *polonicum*	*T. turgidum* ssp. *polonicum*	*T. turgidum*
AB	*T. turanicum*	*T. turgidum* ssp. *turgidum* conv. *turanicum*	*T. turgidum* ssp. *turanicum*	
AB	*T. turgidum*	*T. turgidum* ssp. *turgidum* conv. *turgidum*	*T. turgidum* ssp. *turgidum*	*T. turgidum*
AG	*T. araraticum*	*T. timopheevii* ssp. *armeniacum*	*T. timopheevii* ssp. *armeniacum*	*T. timopheevii*
AG	*T. militinae*			
AG	*T. timopheevii*	*T. timopheevii* ssp. *timopheevii*	*T. timopheevii* ssp. *timopheevii*	*T. timopheevii*
ABD	*T. aestivum*	*T. aestivum* ssp. *aestivum*	*T. aestivum* ssp. *aestivum*	*T. aestivum*
ABD	*T. compactum*	*T. aestivum* ssp. *compactum*	*T. aestivum* ssp. *compactum*	*T. aestivum*
ABD	*T. macha*	*T. aestivum* ssp. *macha*	*T. aestivum* ssp. *macha*	*T. aestivum*
ABD	*T. petropavlovskyi*			
ABD	*T. spelta*	*T. aestivum* ssp. *spelta*	*T. aestivum* ssp. *spelta*	*T. aestivum*
ABD	*T. sphaerococcum*	*T. aestivum* ssp. *sphaerococcum*	*T. aestivum* ssp. *sphaerococcum*	*T. aestivum*
ABD	*T. vavilovii*	*T. aestivum*		
AAG	*T. zhukovskyi*	*T. zhukovskyi*	*T. zhukovskyi*	*T. zhukovskyi*

Molecular results, mainly concerning genome-wide measures of genetic similarity, have also traced the origins of domesticated cereals to wild populations of grasses that are still present in the Fertile Crescent (Heun et al. 1997; Ozkan et al. 2005; Luo et al. 2007; Kilian et al. 2007b), consistent with the independent archaeological evidence.

3.1 Wheat Evolution and Domestication

Studies of wheat evolution have attracted great attention over the past 100 years. Sakamura (1918), Sax and Sax (1924), and Kihara (1924) used cytogenetic methods and recognized that wheat species fall into three groups based upon their ploidy level: (1) diploid $2n = 14$ = einkorn wheat; (2) tetraploid $4n = 28$ = emmer wheats; (3) hexaploid $6n = 42$ = bread wheats. Those cytogenetic studies led to the genome distinctions A, B, D, G, S, and so forth, that are still used today in wheat research. Importantly and uniquely among the cereals, hexaploid bread wheat has no direct hexaploid wild progenitor. It possesses three sets of homoeologous chromosomes, designated as BBA^uA^uDD, whose origins have differing degrees of certainty. The superscript "u" in the A^u genome designation indicates that the A genome is of the type found in *Triticum urartu*.

The D chromosomes stem from wild diploid *Aegilops tauschii* through alloploidization with the wild BBA^uA^u tetraploid *T. dicoccoides* (Kihara 1944). The A^u and B chromosomes derive from hybridization between the wild A^uA^u diploid *T. urartu* and a wild diploid B genome donor (Dvorak et al. 1993; Kilian et al. 2007a), frequently reported to belong to the *Sitopsis* section of *Aegilops*, which includes five species. Brandolini et al. (2006) quantified the genetic relationships among A genomes of wheats by AFLP fingerprinting. Seven AFLP primer combinations produced 239 genome A specific bands for analysis. The results indicate that: (1) the *T. urartu* genome is more closely related to the A genomes of polyploid wheats than to the genome of einkorn (*T. boeoticum*/*T. monococcum*); (2) *T. dicoccon* and *T. durum* cluster together supporting a common origin; (3) hexaploid hulled spelts cluster intermediate between tetraploid and hexaploid wheats; (4) GGA^uA^u wheats cluster distant from both diploid and other polyploid wheats; and (5) the *T. urartu* genome is about 20% more closely related to the A genomes of polyploidy wheats than the *T. boeoticum*/*T. monococcum* genome. *T. timopheevii* is equidistant from those of *T. urartu* and *T. monococcum*.

The tetraploid BBA^uA^u and GGA^uA^u wheats originated through independent allopolyploidization events between two wild diploid grasses. Strong evidence points to the wild outcrossing *Ae. speltoides* (SS) (or a genotype similar to it) as the female parent of tetraploid wheats and to wild *T. urartu* (A^uA^u) as the male parent (Dvorak and Zhang 1990; Huang et al. 2002; Zhang et al. 2002; Kilian et al. 2007a). Kilian et al. (2007a) used a 3-tiered approach. Using 70 amplified fragment length polymorphism (AFLP) loci, they sampled molecular diversity among 480 wheat lines from their natural habitats encompassing all S genome *Aegilops*, the putative progenitors of wheat B and G genomes. Fifty-nine *Aegilops* representatives for S genome diversity were compared at 375 AFLP loci with diploid, tetraploid, and 11 nulli-tetrasomic *T. aestivum* Chinese Spring aneuploids lines: 6 nulliB–tetraD (N1BT1D, N2BT2D, N3BT3D, N4BT4D, N5BT5D, N6BT6D) and 5 nulliB–tetraA (N1BT1A, N2BT2A, N3BT3A, N5BT5A, N7BT7A) (Sears 1954). Nulli-tetrasomic lines are aneuploid genetic stocks that use the compensating ability of homoeologous chromosomes. For example, N1BT1D indicates nulli-tetrasomic lines missing a pair of chromosome 1B that is replaced by an extra pair of chromosome 1D. B genome-specific markers allowed pinning the origin of the B genome to S chromosomes of *Ae. speltoides*, while excluding other lineages.

The outbreeding nature of *Ae. speltoides* influences its molecular diversity and bears upon inferences of B and G genome origins. Haplotypes at nuclear and chloroplast loci *ACC1*, *G6PDH*, *GPT*, *PGK1*, *Q*, *VRN1*, and *ndhF* for ~70 *Aegilops* and *Triticum* lines (0.73 Mb sequenced) reveal both B and G genomes of polyploid wheats as unique samples of *Ae. speltoides* haplotype diversity. These have been sequestered by the BBA^{u}A^u *T. dicoccoides* and GGA^{u}A^u *T. araraticum* lineages during their independent origins. The hybridization which generated the BBA^{u}A^u wheats may have taken place between 0.25 and 1.3 Mya according to some estimates (Mori et al. 1995; Huang et al. 2002; Dvorak and Akhunov 2005), while the event that led to the GGA^{u}A^u wheats likely occurred later (Huang et al. 2002). The distinctly reticulate evolutionary relationships between wheats with different ploidy levels tracing to hybridization events are shown in Fig. 4. The corresponding inflorescence morphologies are shown in Fig. 5.

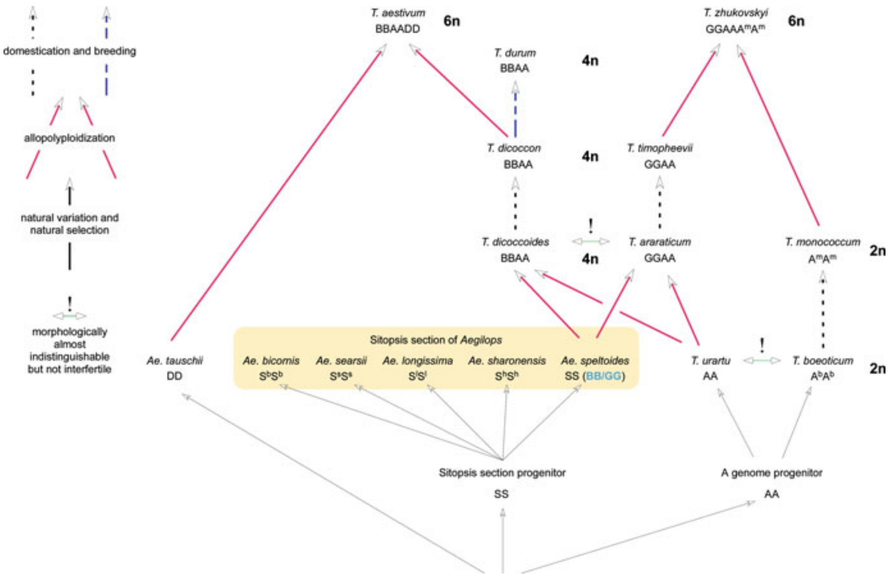

Fig. 4 Overview of wheat evolution and events. This figure has been originally published in Kilian et al. (2007a) (SI). Published with permission from Oxford University Press

Fig. 5 Ears of wheat species and *Aegilops* species involved in wheat evolution. Wheat: wild diploid (*T. urartu*; *T. boeoticum*), domesticated diploid (*T. monococcum*; *T. monococcum aegilopoides*, the feral form of *T. monococcum* is shown at the *right hand side* between *T. boeoticum* and *T. monococcum*), wild tetraploid (*T. dicoccoides*; *T. araraticum*), domesticated tetraploid (*T. dicoccon*; *T. durum*; *T. timopheevii*), hexaploid domesticated (*T. spelta*, *T. aestivum*) and *Aegilops* (*Ae. speltoides*; *Ae. tauschii*). See also Fig. 4

3.1.1 Diploid Wheats

Two wild diploid *Triticum* species are recognized: *T. boeoticum* (A^bA^b) and *T. urartu* (A^uA^u). They are separated by crossing barriers (Johnson and Dahliwal 1976), differ in plant morphology (Gandilian 1972; Dorofeev et al. 1979) and at biochemical and molecular marker loci (Johnson 1975; Dvorak et al. 1998a; Kilian et al. 2007b). The diploid einkorn wheat *T. monococcum* was among the first crops domesticated in the Fertile Crescent starting from the wild progenitor *T. boeoticum*. Domestication has been located to the geographic area of the volcanic Karacadag

Fig. 6 Massive stands of wild einkorn wheat (*T. boeoticum*) in the Karacadag mountain range. Picture taken by H. Özkan in early July 2004

mountain range in south-eastern Turkey (Heun et al. 1997; Fig. 6). The earliest archaeological records from domesticated einkorn are described from Abu Hureyra (Hillman et al. 1989), Cayönü (van Zeist and de Roller 1991–1992), and Nevali Cori (Pasternak 1998). Einkorn was the staple crop of the Sumer populations and has been found in the excavated layers of Troy (Nesbitt and Samuel 1996).

Today, einkorn is a relict crop with only marginal economic importance. During the last 5,000 years, einkorn was largely abandoned and replaced by tetraploid and hexaploid wheats, which deliver higher yields. This circumstance is of particular importance and makes einkorn an outstanding model system for investigating the history of crop domestication with genetic tools, in that domesticated einkorn germplasm is devoid of modern breeding bottlenecks. The term "breeding bottlenecks" refers to the circumstance that most modern cereal varieties are the product of intense breeding efforts particularly during the last 100 years. Because einkorn was never subjected to such breeding programs, Kilian et al. (2007b) reasoned that extensive sampling of genetic diversity among wild and domesticated accessions should discriminate between different hypotheses of cereal domestication, giving insights into the Neolithic domestication of this cereal that are not clouded by breeding bottlenecks that occurred in the last 100 years (the "green revolution").

In that study, Kilian et al. (2007b) investigated nucleotide variation at 18 loci from 92 domesticated einkorn lines compared to 321 lines from wild populations. Several insights into domestication history emerged from that study. One of the most important insights was that wild einkorn is not really a single homogeneous

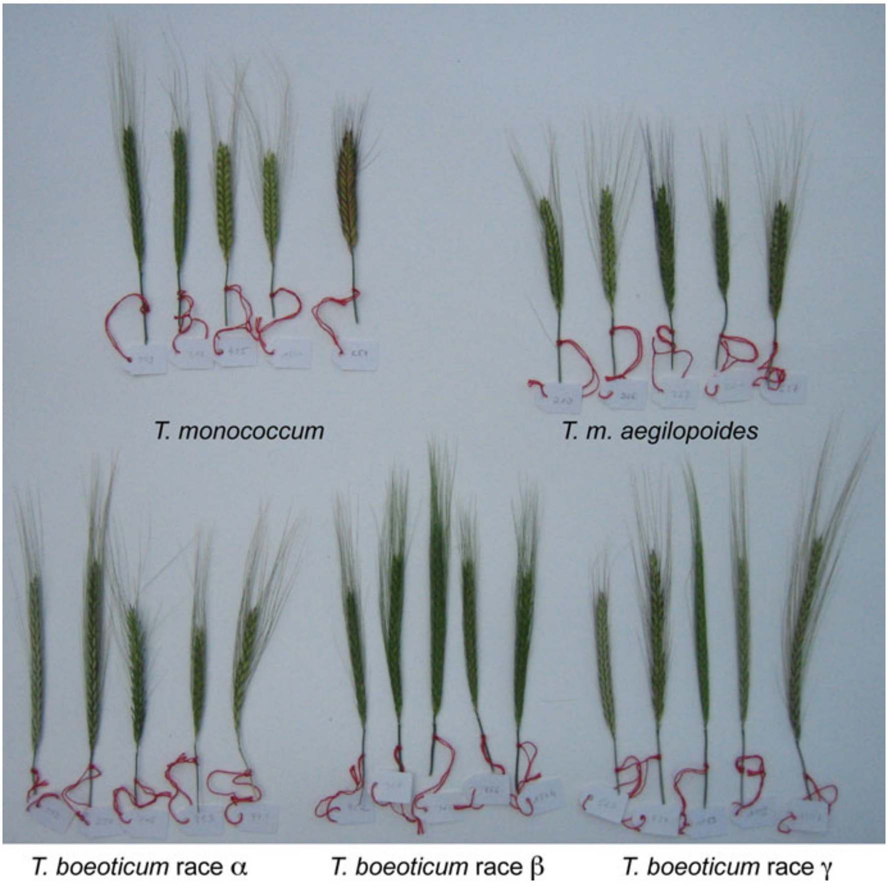

Fig. 7 Ears of einkorn groups. Wild einkorn (*T. boeoticum*) groups are shown at the *bottom*: (race α, race β, race γ), domesticated einkorn (*T. monococcum*) and its feral form *T. monococcum aegilopoides* are shown at the *upper part*

population, rather wild einkorn underwent a natural process of genetic differentiation prior to domestication, resulting in three distinct *T. boeoticum* races (Fig. 7). These three races, which we designated α, β, and γ, are genetically distinct both at the level of their haplotypes across 18 loci studied and at the level of their AFLP fingerprints, but they are morphologically indistinguishable, or nearly so (Fig. 7). One of those races, wild race β, is genetically much more similar to domesticated einkorn, hence it is the race, or genotype, that was exploited by humans during domestication. Race β occurs only in the Karacadag and Kartal-Karadag Mountains. In this sense, the findings are consistent with those of Heun et al. (1997), but extend them significantly and open up further insights into the domestication process.

A second major surprise in the findings of Kilian et al. (2007b) was that nucleotide and haplotype diversity in domesticated einkorn was found to be higher than in the β race. Nucleotide diversity, π, represents the average sequence divergence between all homologous sequences among all individuals in a given set for comparison. It is often used to infer the presence of past population bottlenecks in studies of domestication genetics, because when a population goes through a bottleneck, the allelic diversity in the population is diminished, and π is thus expected to be small. Several studies from the literature have reported evidence to suggest that nucleotide diversity is reduced in domesticated cereals, whence the concept domestication bottlenecks stems (Dubcovsky and Dvorak 2007). However, two points are critical here. First, most studies of cereal domestication entailed the analysis of highly inbred lines – how is one to infer the presence of an ancient domestication bottleneck if the real bottleneck occurred during breeding in the last 100 years? This issue looms over the domestication bottleneck concept in cereal domestication studies. Second, it was therefore all the more surprising that, when we looked for evidence of a breeding bottleneck in domesticate einkorn, a rare case of a cereal in which there have been no recent breeding bottlenecks, we found that there was no reduction of nucleotide diversity at all (Table 3). The absence of a domestication bottleneck is in contrast to the conclusions of studies of domestication in intensely bred crop species, where claims for domestication bottlenecks are commonplace. In nature, wild race β has been sampled only in the "core area" of agricultural development in south-eastern Turkey (Lev-Yadun et al. 2000; Bar-Yosef 2002; Lichter 2007), where the closest wild relatives of einkorn, emmer, barley, rye, chickpea, and lentil still grow (Ladizinsky 1985; Salamini et al. 2002; Ozkan et al. 2005; Abbo et al. 2006). Detailed archaeological reports by Hillman (2000), Willcox (2005), Weiss et al. (2006), and Willcox et al. (2008) describe how the pre-domestication cultivation of (wild) cereals lasted for centuries in the region, and how it was followed by gradual (Kislev 2002) and multiple (Gebel 2004) appearances of domesticated phenotypes. The genetic and cultural

Table 3 Haplotype and nucleotide diversity in wild and domesticate lines. See Kilian et al. (2007b) for further explanations

Species/ssp/race	n[a]	H[b]	Hd[c]	π_{tot}[d]	π_{sil}[d]	θ_{tot}[d]	θ_{sil}[d]
T. boeoticum (wild)	321	114	0.380	4.73	8.51	3.45	4.29
race α	230	77	0.242	3.48	6.37	2.72	3.23
race γ	49	75	0.362	4.59	7.81	4.20	5.27
race β	42	43	0.260	1.56	2.70	2.05	2.15
T. monococcum (domesticate)	84	61	0.278	2.97	5.44	2.45	2.89
T. m. aegilopoides (feral)	8	35	0.353	3.75	6.35	3.45	3.42
T. urartu (outgroup)	39	35	0.276	0.53	0.92	0.66	0.96

Hd Haplotype diversity for selfing species (Nei 1987); π_{tot} average number of nucleotide differences per site between two sequences calculated on the total number of polymorphic sites; π_{sil} average number of nucleotide differences per site between two sequences calculated on the silent sites (synonymous and noncoding positions); θ_{tot} Waterson's estimator per site calculated on the total number of polymorphic sites; θ_{sil} Waterson's estimator per site calculated at silent sites

[a]Number of lines

[b]Number of haplotypes found (gapped sites and the Lr10 locus excluded)

[c]Nei's unbiassed estimate of haplotype diversity for inbreeding species (Nei 1987)

[d]Values of nucleotide diversity Pi (π) and Waterson's estimator (θ) are given 10^3

mechanisms underlying the emergence of those phenotypes are remaining questions (Diamond and Belwood 2003).

If geographically distinct domestication events each entailed a random sampling from local genotypes, and if local populations can be identified based on molecular markers, domesticated lines should trace to different localities across the range of the wild progenitor (Jones 2004). This is not observed for einkorn: the wild race β described in Kilian et al. (2007b) appears to be the sister to domesticated einkorn in the absence of an evident reduction of genetic variation. This can be accommodated by a domestication model that we have called the "dispersed-specific" model (Fig. 8). In essence, in this new scenario, a sedentary society associated with the Mesolithic (12,500–9,500 BC) Natufian culture in the Levante (Bar-Yosef 2002) first harvested and then cultivated β race population(s) of wild einkorn, which was probably distributed to local human settlements in the "core area." Here, at these human settlements, favorable traits have been selected from the β race over the centuries and the β race became adapted to human needs. It is still unclear how much intermixture from other wild einkorn races occurred. In a later phase of agricultural expansion, the β race was transferred to other locations outside the

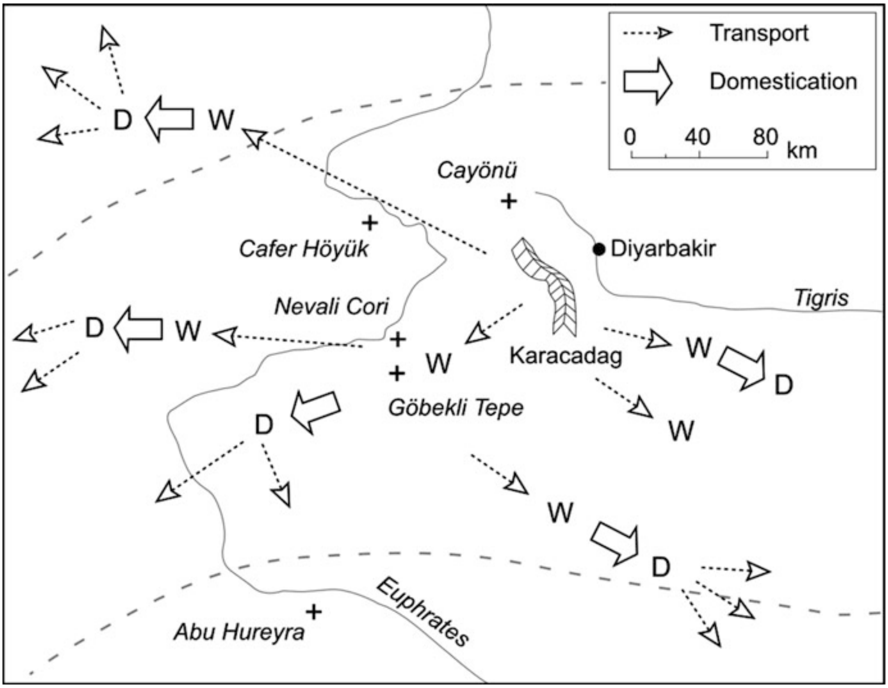

Fig. 8 The dispersed-specific model for einkorn domestication. Selected archaeological sites are indicated in *italics*. The Fertile Crescent is indicated with a *dotted line*. *W* Wild einkorn (β race); *D* domesticated einkorn. This figure has been originally published in Kilian et al. (2007b) (published with permission from Oxford University Press)

"core area," possibly already in a state of nascent domestication. Transport could have involved migrating farmers (Nadel 2002; Renfrew 2002) or exchange of seeds for other goods, as not all soils of the Fertile Crescent were adapted to cereal cultivation (Willcox 2005).

Concerning einkorn, in several areas, variants of the wild β race emerged having common domesticated traits. These domestication events occurred at several places within the "core area" These domestication events were connected with each other due to the same β race seed material used and due to the same human culture, and a genetic bottleneck would have occurred at each domesticating human settlement. However, domestication events at numerous villages would have allowed the newly domesticated lines to integrate a full arsenal of wild haplotypes; in essence, domestication bottlenecks at several human settlements starting from the same genetic pool of the wild β race would have resulted in no domestication bottleneck. In this scenario, the specificities still maintained at a molecular level of the wild β race make it possible to assign the adoption of the wild β race to the Karacadag core area, while the multiple extraction of domesticated lines from the β population has preserved their large genetic variation.

This hypothesis accounts for our molecular data and accommodates the results of archaeological excavations: tools for grinding seeds are present in the majority of Fertile Crescent sites well before the large seed remains of domesticated einkorn wheat (Bar-Yosef 2002), supporting the view that humans in the region were familiar with the harvest of wild seeds both in natural habitats and in cultivated fields (Weiss et al. 2006; Lichter 2007).

Further studies have been carried out on einkorn wheat during the SPP127 project.

Einkorn is cultivated today on a very small scale as feed for poultry and swine in some mountainous villages in Italy, Spain, and Turkey (Nesbitt and Samuel 1996; Perrino et al. 1996). This wheat has been re-discovered as a source of genetic variation for wheat breeding, and it is to some extent used by the food industry in Europe. One example is a recent study on natural variation and identification of micro-elements content in seeds of einkorn wheat (Ozkan et al. 2007). Micronutrient deficiencies in human beings are common problems, especially in developing countries. Among the micronutrient deficiencies, zinc (Zn) and iron (Fe) deficiencies are particularly important severely affecting the health of humans. A major reason for the widespread occurrence of micronutrient deficiencies in human beings is the high and monotonous consumption of cereal-based foods with very low content of micronutrients. An increase in concentration of Zn and Fe in grain is, therefore, a high-priority research area. Exploitation of large genetic variation for Zn and Fe existing in cereals germplasm is an important approach to minimize the extent of Zn and Fe deficiencies in developing countries. In the present study, the variation for seed content of micronutrients (Zn, Fe, Mn, and Cu) in 54 accessions of einkorn wheat (*T. monococcum*) was tested. Additionally, a mapping population comprising 168 recombinant inbred lines has also been tested for seed micronutrient variation and analyzed for QTL identification associated with micronutrient content. The results obtained showed large genotypic variation in micronutrient contents. One major QTL, common to all four microelements and explaining from 10 to 30% of the variation, was observed on chromosome 5.

Wheat is the staple food for about 40% of the world's population. However, celiac disease (CD) is an inflammatory condition characterized by injury to the lining of the small intestine on exposure to the gluten of wheat, barley and rye. The prevalence of CD among Caucasians is in the range of 1:100–300 (Wieser and Koehler 2008). The involvement of gluten in the CD syndrome has been studied in detail in bread wheat, where a set of "toxic" and "immunogenic" peptides has been defined. For wheat diploid species, information on CD epitopes is poor. In a recent paper, Vaccino et al. (2009) have therefore adopted a genomic approach in order to understand the potential CD danger represented by storage proteins in diploid wheat, and they sequenced a sufficiently large number of cDNA clones related to storage protein genes of *T. monococcum*. Four bona fide toxic peptides and 13 immunogenic peptides were found. All the classes of storage proteins were shown to contain harmful sequences. The major conclusion is that einkorn has the full potential to induce the CD syndrome, as already evident for polyploid wheats. In addition, a complete overview of the storage protein gene arsenal in *T. monococcum* was presented, including a full-length HMW x-type sequence and a partial HMW y-type sequence. The information derived from that study strongly argues against the approach of breeding wheat species low in sequences noxious for CD patients by eliminating the immunogenic or toxic epitopes from their storage proteins arsenal; in fact, it seems hardly feasible to create new genotypes lacking all the 17 harmful peptides belonging to different loci. Accordingly, the silencing, via targeted mutagenesis of the genes giving rise to immunostimulatory sequences (Vader et al. 2003) also appears unrealistic.

The second wild diploid *Triticum* species, *T. urartu* (A^uA^u), occurs on basaltic rocks in some parts of the Fertile Crescent (Zohary and Hopf 2000). The species was never domesticated, but played a critical role in wheat evolution. *T. urartu* donated the A genome to all tetraploid and hexaploid wheats (Dvorak et al. 1993; Brandolini et al. 2006; Kilian et al. 2007a; Fig. 4).

3.1.2 Tetraploid Wheats

Two wild tetraploid wheat species are known, *T. dicoccoides* and *T. araraticum*. They are similar in morphology, but different in their genomic constitution: *T. dicoccoides*, has the genomic formula BBA^uA^u and *T. araraticum* GGA^uA^u (Zohary and Hopf 2000). *T. dicoccoides*, or wild emmer, belongs to the first cereals domesticated by humans in the Fertile Crescent and in its domesticated form is known as *T. dicoccon* (emmer, BBA^uA^u). This domestication step provided the key for subsequent bread wheat evolution (Fig. 4). Wild emmer was first discovered in nature in 1906 in eastern Galilee, Israel, by Aaron Aaronsohn (Aaronsohn and Schweinfurth 1906). His studies of geographic distribution and ecological requirements greatly contributed to our current understanding of emmer wheat distribution, diversity, and domestication. Wild emmer nowadays has a more restricted distribution range than wild einkorn, and is recognized today in the western Fertile Crescent, the central part of south-eastern Turkey, and mountain areas in eastern Iraq and western Iran. Several issues concerning geography and domestication of wild emmer wheat were recently reviewed Özkan et al. (2010). The authors considered published molecular and archaeological data and re-analyzed the data of Ozkan et al. (2005). Wild emmer was probably domesticated in south-eastern Turkey (Ozkan et al. 2002, 2005, 2009; Mori et al. 2003; Luo et al. 2007). A reconsideration of the domestication geography of tetraploid wheats has been considered by Ozkan et al. (2005) and by Luo et al. (2007). Phylogenetic analysis indicate that two different races of *T. dicoccoides* exist, the western one, colonizing Israel, Syria, Lebanon, and Jordan, and the central-eastern one, which has been frequently sampled in Turkey and rarely in Iraq and Iran. It is the central-eastern race that has played the role of the progenitor of the domesticated germplasm. This is supported by the results from the collections of Ozkan et al. (2002), Mori et al. (2003), and Luo et al. (2007). A disagreement is nevertheless appearing at the local geographical scale: the chloroplast DNA data indicate the Kartal mountains at the western border of the "core area" (Abbo et al. 2006), while AFLP fingerprinting points to the Karacadag range as the putative site of tetraploid wheat domestication. From this area, emmer expanded across Asia, Europe, and Africa (Dubcovsky and Dvorak 2007). South-western expansion of domesticated emmer generated sympatry with the southern populations of *T. dicoccoides* and the rise of a secondary diversity center (Luo et al. 2007). This was followed by the subdivision of domesticated emmer into northern and southern subpopulations. North-east expansion allowed meeting the distribution of *Ae. tauschii* and, thus, the emergence of hexaploid *T. aestivum*. Genetic evidence suggests that the synthesis of hexaploid wheat took place within the corridor from Armenia to the south-western coast of the Caspian Sea (Dvorak et al. 1998b). Based on the D genome diversity, the synthesis of the hexaploid wheat has been estimated to have occurred at least twice (Dvorak et al. 1998b; Giles and Brown 2006).

Based on a direct estimation of mutation rate for microsatellite loci and re-sequenced candidate loci, Thuillet et al. (2002, 2005) and Haudry et al. (2007) have discussed the occurrence of bottlenecks during tetraploid wheat domestication and breeding. A continuous decrease of effective population sizes is reported, indicating the action of severe bottlenecks, associated in particular to breeding. However, Thuillet et al. (2005) reported that the bottleneck of domestication was relatively low, which in terms of Nei's heterozygosity correspond to the presence of 95% of the diversity in domesticated *T. dicoccon* compared to wild *T. dicoccoides* (but 63.2% of effective population size has been lost from wild to domesticated emmer wheat). This situation is remarkably similar to the one reported for einkorn by Kilian et al. (2007b). On the other hand, important losses of nucleotide diversity are reported at 21 loci from the comparisons of domesticated lines of *T. dicoccon* and *T. durum* with the wild *T. dicoccoides* (Haudry et al. 2007). However, in this experiment, it is difficult to separate recent bottlenecks from the loss of diversity due only to domestication.

Several cultivated tetraploid BBA^uA^u wheats were derived later from the domesticated emmer: *T. carthlicum* (Persian wheat), *T. polonicum* (Polish wheat), *T. ispahanicum, T. turanicum* (Khurasan wheat), and *T. turgidum* (English or pollard wheat). *Triticum dicoccon* was the favored crop for bread-making in ancient Egypt. Like einkorn, emmer wheat cultivation has declined today, and it can be found only in some traditional farming communities mainly in Russia and Ethiopia. Somewhat later, *T. durum* (macaroni or hard wheat) also originated from *T. dicoccon* (Damania 1998; Salamini et al. 2002; Ozkan et al. 2005, 2009), but different opinions exist on this point (Haudry et al. 2007). This naked wheat is widely cultivated today for pasta production.

In the eastern part of the Fertile Crescent, the wild tetraploid wheat *T. araraticum* (Araratian or Armenian wild emmer) substitutes *T. dicoccoides* (Johnson 1975; Zohary and Hopf 2000). While *T. dicoccoides* crosses easily with cultivated tetraploid wheats, *T. araraticum* does not, most probably due to relevant differences in the genome, like the existence of several translocations between B and G chromosomes (Feldman 1966). *Triticum araraticum* was also domesticated, but its cultivated form, *T. timopheevii* (GGA^uA^u; Timopheev's wheat), has been found only in west Georgia together with the hexaploid wheat *T. zhukovskyi* ($GGA^uA^uA^mA^m$; Zhukovskyi's wheat) (Dorofeev et al. 1979). It is speculated that, when emmer cultivation spread to Transcaucasia, local populations of *T. araraticum* were colonizing, as a weed, the fields of emmer crops and, by being incorporated into the agricultural cycle of harvest and sowing, became domesticated (Nesbitt and Samuel 1996).

3.1.3 Hexaploid Wheats–Bread Wheat

Economically, the most important wheat is *T. aestivum* or bread wheat (BBA^uA^uDD). Bread wheat is a temperate crop grown from 67°N in Norway, Finland, and Russia to 45°S in Argentina. *Triticum aestivum* comprises a number of free-threshing forms such as *T. compactum* (club wheat), *T. sphaerococcum* (Indian dwarf or shot wheat), *T. petropavlovskyi* (rice wheat), and *T. tibetanum* (Tibetan wheat). Other forms are hulled: *T. spelta* (Dinkel or large spelt), *T. macha*, *T. vavilovii*, and *T. yunnanense* (Dvorak et al. 1998a). No wild hexaploid wheat has ever been found, only a semi-wild weedy form of hulled and brittle hexaploid wheat, *T. tibetanum*, has been discovered in Tibet (Shao et al. 1983). It is accepted that *T. aestivum* originated from a cross between domesticated hulled tetraploid emmer *T. dicoccon* (or the free-threshing hard wheat *T. durum,* or the free-threshing *T. parvicoccum*) and the goat grass *Aegilops tauschii* (DD) (Kihara 1944; McFadden and Sears 1946; Kerber 1964; Kislev 1980; Dvorak et al. 1998a; Matsuoka and Nasuda 2004). This cross should have taken place after emmer or hard wheat cultivation spread east from the Fertile Crescent into the natural distribution area of *Ae. tauschii*. The cross occurred most probably south or west of the Caspian Sea about 8,000 years ago (Nesbitt and Samuel 1996; Salamini et al. 2002; Giles and Brown 2006). *Aegilops tauschii* encompasses several morphological varieties that are roughly grouped into *Ae. tauschii* ssp. *tauschii* and *Ae. tauschii* ssp. *strangulata* (Kihara et al. 1965; Jaaska 1995; Dvorak et al. 1998a). Several studies show that *Ae. tauschii* ssp. *strangulata* provided the wheat D genome (at least twice), but contributions from both subspecies have also been discussed (Nishikawa et al. 1980; Jaaska 1981; Dvorak et al. 1998b; Talbert et al. 1998). If only a few *Ae. tauschii* genotypes participated in the origin of *T. aestivum*, this polyploidization should have been accompanied by a reduction of diversity (Haudry et al. 2007). However, high mutation rates, together with buffering effects caused by polyploidy, should enable hexaploid wheat to enhance diversity (Dubcovsky and Dvorak 2007).

One still unsolved important question is the origin of the hulled hexaploid wheat *T. spelta* or spelt (McFadden and Sears 1946; Kuckuck and Schiemann 1957; Kuckuck 1959; Nishikawa et al. 1980; Dvorak et al. 1998a; Salamini et al. 2002; Blatter et al. 2004). Two types of spelts are known: the Asian and European spelts. Whether *T. spelta* origin is monophyletic or polyphyletic is still open to debate (Nesbitt and Samuel 1996; Dvorak and Luo 2001; Blatter et al. 2004). Genetic data suggest that the hulled hexaploid wheats are more primitive than the free-threshing forms. This hypothesis, however, is not supported by archaeological findings because free-threshing forms occured earlier than the hulled ones. Hulled wheat appeared in central Europe in the Early Bronze Age (summarized in Nesbitt 2002) and 7,000-year-old remains are found in northern Iraq (Kislev 1984). Free-threshing wheat, in turn, has been found in Can Hassan III dating to 8,500 years ago (Hillman 1978) and at Cafer Höyük dating to 8,000–9,000 years ago (summarized in Salamini et al. 2002). The origin of hulled hexaploid wheat remains controversial.

3.2 Barley Evolution and Domestication

Hordeum vulgare (barley) was domesticated from its wild progenitor *H. spontaneum*. Like wheats, barley belongs to the oldest and most important crops of the Fertile Crescent (Takahashi 1955; Jaaska 1998; Zohary and Hopf 2000; Badr et al. 2000; Bothmer von et al. 2003; Pourkheirandish and Komatsuda 2007). Barley varieties are either two-rowed or six-rowed, based on type of ear. The species is more drought tolerant and much more salt tolerant than wheat. The crop was very important in some regions of the Fertile Crescent, the main crop in Mesopotamia, and a primary cereal in ancient Egypt (Harlan 1995).

Wild barley grains have been found in several pre-agricultural Pre-Pottery Neolithic sites. The earliest evidence is from Ohalo II, located at the shore of the Sea of Galilee, where 21,000-year-old wild remains were found in large amounts (Kislev et al. 1992). This supports the conclusion that wild barley has been collected from nature long before domestication. The earliest carbonized remains of domesticated barley are of the two-row type (van Zeist 1970; Hillman et al. 1989), but six-row types appear already at Ain Ghazal around 9,000–8,500 years ago (Rollefson et al. 1985; Willcox 1998). Domesticated barley later spread with other crops through the Mediterranean to Europe and Africa, and eastwards through Iran and Afghanistan into India and China.

Wild barley *H. spontaneum* has a wider distribution than any wild wheat. It is present all over the Fertile Crescent because the species is a colonizer of disturbed agricultural habitats. The species occurs in the eastern Mediterranean and western Asia and reaches Turkmenia and Afghanistan in the east (Harlan and Zohary 1966). A few wild barley populations are also found in secondary habitats such as Morocco and Abyssinia.

Considerable studies have been invested in studying barley diversity and identifying the region of barley domestication. Badr et al. (2000) originally reported the monophyletic nature of barley domestication based on allelic frequencies at 400 AFLP polymorphic loci studied in 317 wild and 57 domesticated lines. The wild populations from Israel–Jordan were more similar than any others to the domesticated gene pool. The results supported the hypothesis that the Israel–Jordan area was the region in which barley was brought into culture. Moreover, the diagnostic allele I of the homeobox gene *BKn-3* [*Knotted-1*-like-homeobox (*Knox*) gene class], rarely but almost exclusively found in Israeli *H. spontaneum*, was pervasive in western landraces and modern cultivated varieties. In landraces from the Himalayas and India, the *BKn-3* allele IIIa prevails, indicating that an allelic substitution has taken place during the migration of barley from the Fertile Crescent to south Asia. Thus, the Himalayas can be considered a region of domesticated barley diversification. Other reports point to further domestication sites and to different origins (Schiemann 1939; Åberg 1940; Bekele 1983; Molina-Cano et al. 1987; Zohary and Hopf 2000; Molina-Cano et al. 2005; Morrell and Clegg 2007; Orabi et al. 2007; Azhaguvel and Komatsuda 2007; Saisho and Purugganan 2007). Allaby and Brown (2003, 2004) questioned the use of AFLP markers in phylogenetic studies addressing crop domestication. Subsequently, Salamini et al. (2004) cited several dozens of papers that correctly addressed domestication issues based on AFLP markers.

Studies based on molecular markers comparing wild to domesticated barley have shown that a large amount of nucleotide diversity has been lost in current domesticated varieties (Russell et al. 2004; Caldwell et al. 2006; Kilian et al. 2006; Morrell and Clegg 2007). Kilian et al. (2006) determined, for a representative sample of 20 domesticated barley (*H. vulgare*) lines and 25 wild *H. spontaneum* lines, the haplotypes at seven loci – *Adh2*, *Adh3*, *Amy1*, *Dhn9*, *GAPDH*, *PEPC*, and *WAXY*. The number of haplotypes, average nucleotide diversity, π, and Watterson's theta at silent sites was reduced in domesticated lines. Two loci, *Amy1* and *PEPC*, were monomorphic in domesticated lines, while *Amy1* and *GAPDH* produced significant values of Tajima's D when all domesticated and wild lines were considered. At *GAPDH*, π was slightly higher in domesticated than wild forms, due to divergent high-frequency haplotypes; for the remaining six loci, 87% of nucleotide diversity has been lost in the domesticated forms. Bottlenecks acting on neutrally evolving loci either during the domestication process or during subsequent breeding, or both, are sufficient to account for reduced diversity and the results of Tajima's test, without the need to evoke selection at these loci.

The domesticated varieties considered, although all sampled were among those currently cultivated in Turkey, were shown to share the same molecular and morphological variability as larger samples of barley genotypes, indicating that the conclusions reported are of general value for this crop.

Recent data have agreed with the conclusion that two-row and six-row genotypes may have different, independent origins (Zohary and Hopf 2000; Kilian et al. 2006; Komatsuda et al. 2007). These new findings are nevertheless in agreement with the previously inferred area of barley domestication in the Jordan valley (Badr et al. 2000). The new data open up the possibility that barley domestication might have occurred independently separate occasions. This conclusion would not be consistent with the conclusions of Badr et al. (2000), but is favored other authors, including Molina-Cano et al. (2005), Kolodinska Brantestam et al. (2004), Casas et al. (2005), Tanno and Takeda (2004); Komatsuda et al. (2004), Taketa et al. (2004), and Komatsuda et al. (2004). The particular matter concerning single versus multiple origins of barley is, however, complicated by the fact that: (1) multiple independent introgressions of genes from wild relatives to cultivated varieties can mimic multiple domestication events (Badr et al. 2000; Kanazin et al. 2002; Abdel-Ghani et al. 2004); and (2) splitting of domesticated genotypes in two alternative groups based on two- or six-rowed ears, hulled or naked caryopsis, western or eastern varieties, and brittleness of the rachis might have followed the domestication process, rather than being coeval with it.

4 Conclusions and Final Considerations

Archaeological and genetic evidence indicate that western agriculture began in the Fertile Crescent about 12,000 years ago (Zohary and Hopf 2000; Kilian et al. 2009). The present view is that the process of crop domestication was slow, spanned several centuries, and entailed repeated domestication events (Tanno and Willcox 2006). Local wild wheat populations were domesticated in a “core area” of the Fertile Crescent and were then gradually dispersed throughout the region (Abbo et al. 2006). Nearly all current domestication models predict a reduction in genetic diversity in domesticated forms compared to their wild progenitors (Doebley et al. 2006). However, recent work of Kilian et al. (2007b) with wild and domesticated einkorn wheat shows no reduction of diversity that could be attributable to the domestication process, raising the issue of whether previous inference of “domestication bottlenecks” in other cereals might in fact be instead breeding bottlenecks.

The keys to obtaining deeper insights to plant domestication are several-fold. First, comprehensive germplasm reference collections covering the whole distribution area for each species are needed, meaning that the natural habitats of the wild progenitors throughout the Fertile Crescent need to be more thoroughly sampled. Studies of domestication genetics need to encompass many wild and domesticated accessions for each species, otherwise sampling effects may severely bias the results. If the goal is to identify the closest relatives among wild progenitors, the diversity and, in the case of einkorn, the previously unrecognized genetic structure of the wild gene pool needs to be accurately assessed. With the new generation of high throughput sequencing technologies in hand (Goldberg et al. 2006; Wicker et al. 2006), the pace of progress can be expected to accelerate. From the more practical perspective, new genomic resources for future plant breeding continually need to be developed, and agronomically important genes also need to be isolated from the wild genetic reserves, and it is clear that such activities will entail international consortia. Continued improvement of analytical methods addressing domestication issues based on mathematical and statistical models is needed (Pluzhnikov and Donnelly 1996; Thuillet et al. 2005; Haudry et al. 2007; Allaby et al. 2008), as are further excavation campaigns in different archeological sites in the Fertile Crescent, such as Göbekli Tepe or Jerf el Ahmar (Schmidt 2001; Neef 2003; Schmidt 2006; Willcox et al. 2008). In the not too distant future, we can expect new insights into the questions of how humans performed the most important breeding experiment in history 10 millennia before the discovery of genetics.

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List of our publications resulting from the SPP 1127

Vaccino P, Becker H-A, Brandolini A, Salamini F, Kilian B (2009) A catalogue of *T. monococcum* genes encoding toxic and immunogenic peptides for celiac disease patients. Mol Genet Genom 281:289–300

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Invited Lectures and Data Presented from the SPP 1127

05/2003	Bad Honnef, DFG SPP1127 “Radiations: origins of biological diversity”
09/2003	Wernigerode, DFG SPP1127 “Radiations: origins of biological diversity”
05/2004	Bad Honnef, DFG SPP1127 “Radiations: origins of biological diversity”
07/2005	University of Cukurova, Adana, Turkey
08/2005	Udmurt State University, Izhevsk, Russia
09/2005	Bad Honnef, DFG SPP1127 “Radiations: origins of biological diversity”
09/2005	MPIZ Cologne
10/2006	5. Plant Genomics European Meetings, Venice, Italy
08/2007	MPIZ Cologne
11/2007	IPK Gatersleben
01/2008	University Kassel
04/2008	Systematics 2008, Göttingen, two talks
06/2008	Bad Honnef, DFG SPP1127 “Radiations: origins of biological diversity”
06/2008	EPSO Conference 2008, Toulon, France
09/2008	Harlan II (Biodiversity in Agriculture: Domestication, Evolution, & Sustainability) University of California, Davis, USA
10/2008	GPZ Göttingen (German Society of Plant Breeding), Kurt-von-Rümker Symposium
10/2008	University Halle, Department of Botany

Conferences Attended and Data Presented from the SPP 1127

10/2006	5. Plant GEMs Venice, Italy
04/2007	Aaronsohn-ITMI Conference, Tiberias, Israel
04/2008	Systematics 2008, Göttingen, Germany
06/2008	EPSO Conference 2008, Toulon, France
09/2008	Harlan II, US Davis, California, USA
10/2008	GPZ Symposium “Biodiversity in Plant Production” (German Society of Plant Breeding), Göttingen, Germany

Collaborations Resulted from the SPP 1127

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