

Genetic diversity, evolution and domestication of *Triticeae* in the Fertile Crescent

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Wild wheats in the Karacadag mountain range in South-East Turkey (Picture: Hakan Özkan)

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Chapter 1

General introduction and scope of the thesis

“For the sake of future generations, we MUST collect and study wild and weedy relatives of our cultivated plants as well as the domesticated races. These sources of germplasm have been dangerously neglected in the past, but the future may not be so tolerant. In the plant breeding programs of tomorrow we cannot afford to ignore *any* source of useable genes.”

J. R. Harlan (1970)

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 important 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 Globally, wheat is the second most widely produced crop, just recently superseded by maize, while barley ranks fourth in the world after maize, wheat and rice (<http://faostat.fao.org/>; <http://www.croptrust.org>). Wheat and barley are the most important staple crops of Europe and the western part of Asia. Wheat is mainly used for bread and pasta, barley is mainly used as fodder and for brewing beer, rye for fodder and bread.

Human history in Europe is closely interwoven with these three staple crops, because wheat and barley (and possibly rye) belong to the Neolithic founder crops that built western agriculture some 12,000 years ago.

Origins of cultivated plants and agriculture – a brief historical overview

The origins of cultivated plants and their domestication have been of large interest beginning with the landmark essays of Alexander von Humboldt “Essai sur la géographie des plantes” (Humboldt von 1806; Fiedler and Leitner 2000), of Charles Darwin “The origin of species” (Darwin 1859) and “The variation of animals and plants under domestication” (Darwin 1868); and of Alphonse de Candolle “Origine de plantes cultivées” in 1882 (Candolle de 1882; Damania 1998).

De Candolle studied biogeography of cultivated crops and indicated three regions where plant domestication may have taken place: Southwest Asia, China and Tropical Asia. He found that historic events such as glaciations and domestication had paramount importances for crop plant distribution (Candolle de 1882). He identified archaeological, botanical, historical and linguistic evidences that could help to determine the origin of plant domestication (Gepts 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 then summarized all his work on diversity in 1935 in “The phytogeographical basis for plant breeding” (Vavilov 1935) in which he describes eight centers, including a Mediterranean Center where wheats, barleys, vegetables and fruits originated (Hawkes 1998). Vavilov undertook more than one hundred collecting missions and expeditions the results of which are presented in the comprehensive collection by the All-Russian Scientific Research Institute of Plant Industry (VIR) (<http://www.vir.nw.ru>).

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, which he also 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’” and not in the valleys of the large rivers (Braidwood and Braidwood 1950; Braidwood 1972; Braidwood et al. 1983). The term “Fertile Crescent” stems in turn from James Henry Breasted (Breasted 1938; Braidwood 1972).

Archaeological evidence cannot provide all pieces of the puzzle and contributions from related research fields, like archaeobotany or botany, are valuable and contributed to our recent knowledge (Harlan and Zohary 1966; Harlan 1971; Harlan 1975; Hillman and Davies 1990; Harlan 1995; Nesbitt 1995; Nesbitt and Samuel 1996; Willcox 1996; Zohary 1999; Hillman 2000; Nesbitt 2002; Willcox 2005; Tanno and Willcox 2006).

For more than two decades now, molecular biology is providing an increasing amount of new information on genetic diversity of crop plants in relation to their wild relatives, on centers of domestication, on the time frame of the domestication process and on specific alleles that underlie domesticated traits using various molecular markers.

The connection between molecular markers and domestication geography was forged by Heun et al. (1997) who located the origin of einkorn wheat domestication to the Karacadag mountain area in South East Turkey using amplified fragment length polymorphism (AFLP) as molecular marker. That work stimulated the search for the origin of agriculture in related research fields. Other important contributions using different molecular markers for other species followed: barley (Badr et al. 2000); emmer (Ozkan et al. 2002); maize (Wright et al. 2005); rice (Londo et al. 2006) and sorghum (Hamblin et al. 2006).

The development of new molecular fingerprinting techniques, such as single-nucleotide polymorphisms (SNPs) and new generation highthroughput sequencing technologies such as 454-sequencing (Goldberg et al. 2006; Wicker et al. 2006) have brightened the prospects of our staple crops for future requirements.

Evolution and domestication of wheat and barley

Archaeological, phytogeographical, and genetic evidence indicates that western agriculture originated in the Fertile Crescent somewhat 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).

Archaeological evidence showed the occurrence of (mostly charred) plant remains at different excavation sites, in different stratigraphic layers and in different amounts and sizes - that can be analyzed and radiocarbon dated (Hillman 2000). On the other hand, phytogeographical, botanical and genetical studies have identified the wild progenitors of crop plants, their distribution areas and showed their significant morphological and genetical differences (Zohary and Hopf 2000).

It is widely accepted today that western agriculture originated in a “core area” in South East Turkey, where all wild forms of the founder crop package (table 1) overlap and where they still exist today (Lev-Yadun et al. 2000; Abbo et al. 2006). From there, farming spread throughout Europe, Asia and Africa, together with various domesticated plants and animals, and agricultural techniques (Ammerman and Cavalli-Sforza 1984; Nesbitt 2002). The domestication process was slow and lasted up to one millennium in the region (Tanno and Willcox 2006), with autonomous cultivation long before domestication (Weiss et al. 2006).

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Molecular findings, on the basis of genome-wide measures of genetic similarity, have traced the origins of domesticated cereals to wild populations of naturally occurring grasses that still persist in the Fertile Crescent (Heun et al. 1997; Badr et al. 2000; Ozkan et al. 2002; Mori et al. 2003; Ozkan et al. 2005; Luo et al. 2007).

Documenting the number of domestication events, the spread of domesticates and population genetic-related questions are open questions that can be addressed with molecular techniques.

Wild progenitors of Neolithic founder crops

Cultivated cereal crops differ from their wild relatives in several traits, some of them apparently consciously selected by humans. The most important traits modified by domestication are free-threshing habit and brittle rachis. Further traits are photoperiod, vernalization, heading date, plant height, erect plant type, tillering, seed size, grain hardness and seed dormancy (Salamini et al. 2002; Pozzi and Salamini 2007).

Archaeological evidence indicates that plant remains of seven domesticated species occur together at the same sites and at about the same time. It is therefore expected that these species were domesticated together in a “founder package” (Lev-Yadun et al. 2000). The wild and domesticated species of the Neolithic founder package are shown in table 1.

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

Name	Wild progenitor	Domesticated
Einkorn wheat ^a	<i>Triticum boeoticum</i> Boiss. emend. Schiem.	<i>T. monococcum</i> L.
Emmer wheat ^b	<i>Triticum dicoccoides</i> (Körn.) Aarons.	<i>T. dicoccum</i> Schübl.
Barley	<i>Hordeum spontaneum</i> C. Koch	<i>H. vulgare</i> L.
Lentil	<i>Lens orientalis</i> (Boiss.) Hand-Mazz.	<i>L. culinaris</i> Medik.
Pea	<i>Pisum humile</i> Boiss. & Noë	<i>P. sativum</i> L.
Chickpea	<i>Cicer reticulatum</i> Ladiz.	<i>C. arietinum</i> L.
Bitter vetch	<i>Vicia ervilia</i> (L.) Willd.	<i>V. ervilia</i> (L.) Willd.
Flax	<i>Linum bienne</i> Mill.	<i>L. usitatissimum</i> L.

^a It is still unclear yet, if *T. urartu* was also domesticated, because seeds of *T. urartu* and *T. boeoticum* cannot be distinguished.

^b Some evidence supports that wild *Triticum araraticum* Jakubz. was domesticated into *T. timopheevii* (Zhuk.) Zhuk., but the distinguishing between the plant remains of wild *T. dicoccoides* and those of wild *T. araraticum* on one hand, as well as distinguishing between their domesticates at the other hand, are impossible.

Wheat classification and distribution

Wheat evolution has received great interest over the past 100 years, because of its great economic significance. Sasakuma (1918), Sax and Sax (1924) and Kihara (1924) with cytogenetic methods recognized that the wheat species fall into three groups based upon their ploidy level: I) diploid $2n = 14$ = einkorn wheat; II) tetraploid $4n = 28$ = emmer wheats; III) hexaploid $6n = 42$ = bread wheats.

Wild relatives and their crop descendants (table 1) show marked phenotypic differences, collectively

called the “domestication syndrome” (Hammer 1984; Pozzi and Salamini 2007). As a consequence, they have been classified sometimes as different species. This is unjustified in the strict sense, because they are interfertile and this also led to considerable taxonomic inconsistency. During the years several wheat classifications were developed based upon different views, mostly by geneticists (see: <http://www.k-state.edu/wgrc>). One overview on different recent wheat classification systems is presented in table 2. For wheat the latest comprehensive, systematic overview was completed in 1979 by Dorofeev and colleagues. This work was published in Russian and was therefore not recognized globally, but the translation into English is currently underway. The translated version will become a standard for wheat classification and will in turn contribute to eliminate controversial issues. In this thesis the nomenclature and the genome formula of *Triticum* by Dorofeev et al. (1979) and the *Aegilops* nomenclature based on van Slageren (1994) is followed.

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

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

Diploid wheats

Two wild diploid *Triticum* species are recognized today: *T. boeoticum* (A^bA^b) and *T. urartu* (A^uA^u). They are separated by crossing barriers (Johnson and Dhaliwal 1976), and differ in their plant morphology (Gandilian 1972; Dorofeev et al. 1979) and in biochemical and molecular marker loci (Johnson 1975; Dvorak et al. 1998a; Heun et al. 1997).

T. boeoticum or wild einkorn wheat is thought to have been domesticated around the volcanic Karacadag mountain range in South East Turkey into *T. monococcum* (A^mA^m) (Heun et al. 1997). The earliest archaeological records from domesticated einkorn are described from Abu Hureyra (Hillman et al. 1989), Cayönü (Zeist van and de Roller 1991-2) and Nevali Cori (Pasternak 1998). Einkorn was the staple for the

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Shumer culture and was also found in Troy (Nesbitt and Samuel 1996); but is a relict crop today. Einkorn is still cultivated in small scale as a feed for poultry and swine in some mountainous villages in Italy, Spain, Turkey and elsewhere (Nesbitt and Samuel 1996; Perrino et al. 1996). However, einkorn has been rediscovered recently as genetic source for wheat breeding and it is also increasingly used in the natural foods industry.

T. urartu was never domesticated, but this species played a critical role in wheat evolution. *T. urartu*, in fact donated the A genome to all tetraploid and hexaploid wheats (Dvorak et al. 1993).

Tetraploid wheats

Two wild tetraploid wheat species are known – *T. dicoccoides* and *T. araraticum*. They are similar in plant morphology, but they differ in their genomic constitution: *T. dicoccoides* (A^uA^uBB) and *T. araraticum* (A^uA^uGG) (Zohary and Hopf 2000).

T. dicoccoides or wild emmer has a more restricted distribution range than wild einkorn and in nature it grows especially in the western part of the Fertile Crescent. Wild emmer wheat was the first time discovered in nature by Aaron Aaronsohn (Aaronsohn and Schweinfurth 1906) and was domesticated into *T. dicoccum* (emmer, A^uA^uBB) probably also close to the Karacadag mountains in South East Turkey (Ozkan et al. 2002; Mori et al. 2003; Ozkan et al. 2005; Luo et al. 2007). Several other cultivated tetraploid A^uA^uBB wheats have derived later from domesticated emmer: *T. carthlicum* (Persian wheat), *T. polonicum* (Polish wheat), *T. ispahanicum*, *T. turanicum* (Khurasan wheat) and *T. turgidum* (English wheat or pollard wheat). *Triticum dicoccum* was favored 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) possibly derived also from *T. dicoccum* (Damania 1998). This naked wheat is widely cultivated today in the Mediterranean for making pasta.

In the eastern part of the Fertile Crescent, the wild tetraploid wheat *T. araraticum* (Araratic 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 several translocations between the B and G genomes (Feldman 1966). *Triticum araraticum* was also domesticated but its cultivated form, *T. timopheevii* (A^uA^uGG; Timopheev's wheat) was only found in West Georgia together with the hexaploid *T. zhukovskyi* (A^mA^mA^uA^uGG; Zhukovskyi's wheat) (Dorofeev et al. 1979). It is speculated that when emmer cultivation spread to Transcaucasia, local populations of *T. araraticum* could have grown as a weed of emmer crops and, by being incorporated into the agricultural cycle of harvest and sowing, became domesticated (Nesbitt and Samuel 1996).

Extensive research and discussions are still ongoing on the origin of tetraploid wheats. It is currently thought that tetraploid wheats originated through allopolyploidization between two wild diploid grasses. Strong evidences points to wild *Aegilops speltoides* (SS) (or similar to it) as the female parent and to wild *T. urartu* (AA) as the male parent (Dvorak and Zhang 1990; Zhang et al. 2002). It is also thought that the hybridization that led to the A^uA^uBB wheats occurred earlier than the cross towards to the A^uA^uGG wheats (Huang et al. 2002).

Hexaploid wheats

The most economically important wheat is *Triticum aestivum* or bread wheat (A^uA^uBBDD). Bread wheat is a temperate crop and grows with high yields from 67° North in Norway, Finland, and Russia to 45° South in Argentina. In the tropics it only thrives in the highlands (<http://www.croptrust.org>).

T. 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. tibeticum* (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 been ever found and it is accepted that *T. aestivum* originated from a cross between the tetraploid domesticated emmer *T. dicoccum* (or the hard wheat *T. durum*) and the goat grass *Aegilops tauschii* (DD) (Kihara 1944; McFadden and Sears 1946; Matsuoka and Nasuda 2004), after emmer or hard wheat cultivation spread east by farmers into the natural distribution area of *Ae. tauschii*. It is thought that this cross occurred South or West of the Caspian Sea about 8000 years ago (Salamini et al. 2002).

Aegilops tauschii encompasses several morphological varieties which are roughly grouped into two, *Ae. tauschii* ssp. *tauschii* and *Ae. tauschii* ssp. *strangulata* (Kihara et al. 1965; Jaaska 1995; Dvorak et al 1998a). Several studies showed that *Ae. tauschii* ssp. *strangulata* provided the wheat D genome, but contributions from both subspecies are discussed (Nishikawa et al. 1980; Jaaska 1981; Dvorak et al 1998b).

One still unsolved important question today is the origin of hulled hexaploid *T. spelta* or spelt (McFadden and Sears 1946; Kuckuck and Schiemann 1957; Kuckuck 1959; Dvorak et al 1998; Salamini et al. 2002; Blatter et al 2004). Some archaeological and genetic findings suggest that spelt may have been derived by hybridization between free-threshing *T. aestivum* and hulled *T. dicoccum*. Whether *T. spelta* is monophyletic or polyphyletic is also open to debate (Jaaska 1978; Nesbitt and Samuel 1996; Blatter et al. 2004).

Barley classification and distribution

Hordeum vulgare (barley) was domesticated from its wild progenitor *H. spontaneum* and belongs to the oldest and most important crops in the Fertile Crescent (Takahashi 1955; Jaaska 1998; Zohary and Hopf 2000; Badr et al. 2000; Pourkheirandish et al. 2007). Barley is mainly differentiated into two-rowed and six-rowed varieties, by the number of kernels per row and ear. Barley is more drought tolerant and much more salt tolerant than wheat and at one time it has been the most important crop, at least in some regions, in the Fertile Crescent. It was the main crop in Mesopotamia (especially in the south after the salinity increased) and it was also very important in ancient Egypt (Harlan 1995).

Wild barley grains have been found in several pre-agrarian PPN sites. The earliest evidence comes from Ohalo II, located at the shore of the Sea of Galilee, where about 20,000 years old remains have been found in large amounts (Kislev et al. 1992). This indicates that wild barley has been collected from nature long before domestication. The earliest carbonized remains of domesticated barley are of the two-row type (Zeist van 1970; Hillman et al. 1989), but six-row types appear already at Ain Ghazal around 9000-8500 before present (Rollefson et al. 1985; Willcox 1998). Domesticated barley later spread with other crops through the Mediterranean to Europe and Africa (Morocco and Abyssinia), and eastwards through Iran and Afghanistan into India and China.

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Wild barley *H. spontaneum* has a much wider distribution than any wild wheat and is found all over the Fertile Crescent, also because the species is a typical colonizer. The species occurs in the eastern Mediterranean, western Asia and reaches Turkmenia and Afghanistan in the east (Harlan and Zohary 1966). Furthermore, few wild barley populations are known from secondary sites from Morocco and Abyssinia, possibly introduced with other crops (Badr et al. 2000).

Considerable work has been invested to study barley diversity and to identify the region of barley domestication (Schieman 1939; Åberg 1940; Bekele 1983; Molina-Cano et al. 1987; Zohary and Hopf 2000). Molecular evidence is also contradictory. They point to different domestication sites and different origins (Badr et al. 2000; Molina-Cano et al. 2005; Morrell and Clegg 2007; Orabi et al. 2007; Azhaguvel and Komatsuda 2007). At least, it seems generally accepted that two-row and six-row barleys have different, independent origins (Zohary and Hopf 2000; Komatsuda et al. 2007). Different studies using molecular markers and comparing wild versus domesticated barley, further showed that a large amount of nucleotide diversity has been lost in domesticate barleys (Russell et al. 2004; Caldwell et al. 2006; Morrell and Clegg 2007). However, these are only preliminary studies, because only few wild and domesticated lines and few loci have been considered so far. Screening large germplasm collections at more loci is needed.

Scope of this study

The main aim of the study 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.

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Chapter 2

Evolutionary history of wheats - the main cereal of mankind

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Abstract

An attempt in integrating the results of different comparative-genetic analyses of wheats and their molecular taxonomy has been made; the correspondence of earlier evolutionary specifications to the phylogeny within the genus *Triticum* species has been estimated. The relationships have been established based on chloroplast and nuclear DNA sequence data. One phylogenetic tree has been constructed based on the chloroplast sequences and several phylogenetic groups have been found within the genera *Triticum* and *Aegilops*. It has been shown that *Aegilops speltoides* was a donor of the plasmon for all polyploid wheat species, whereas the chloroplast genomes of the diploid *Triticum* species are close to other *Aegilops* species. Nuclear *Acc1* and *Pgk1* genes have been used as the molecular markers for the A and B genomes of the *Triticum* species. No variability has been found in these genes within polyploid wheats. In contrast, three variants of these genes have been detected in diploid A genome *Triticum*. The detailed analysis showed that one of these variants was a progenitor for all A genomes of all polyploid *Triticum* species; the second variant is close to the B genomes of *Ae. speltoides*; and the third one is unique for wild diploid wheats. The inheritance of two domesticated and taxonomically important characters was studied in the ancient hexaploid wheat *Triticum antiquorum*. It was shown that the recessive gene controlling spherical grain was allelic to the s gene determining the same character in the endemic Indian species *T. sphaerococcum*. The dominant genes of *T. antiquorum* and *T. sphaerococcum* controlling compact ears were proved to be nonallelic to the corresponding *T. compactum* gene. Results of molecular analysis indicated on close relationship of all hexaploid wheat species.

Introduction

Annual, self-pollinated coarse-grained plants spread over vast territories in Mediterranean climate. Their grains are “convenient” for intensive gathering and, what is not less important, for long-term preservation. The transition from gathering wild cereals towards modern plant breeding is complex and still a matter of discussion.

The history of cultivated plants is closely interwoven with that of mankind. Many investigations based on genetic, comparative-genetic, molecular, archaeological and geobotanical analysis have succeeded in identifying the progenitors of cultivated species, their phylogeny and place of domestication (Goncharov et al. 2007). Independent domestications of four main cereals wheat, barley, rice and maize produced similar results (Harlan 1992). The earliest signs of domestication appear in Pre-pottery Neolithic B (Nesbitt 2001). Archeological data provided evidence that barley (*Hordeum* ssp.) and wheat (*Triticum* ssp.) were among the first domesticated plants. Their cultivation was commenced on the threshold of late Stone Age (Nesbitt 2001).

In the course of time, wheats became the main cultivated crop covering the largest area among all cultivated plants. Curiously, diploid cultivated einkorn wheat *Triticum monococcum* L. was the basic crop of the Shumer culture, whereas tetraploid emmer wheat *T. dicoccum* was cultivated in ancient Egypt.

De Candole (1885) already considered the problem on the origin of wheat species separately having no data for resolving this point on the origin of cultivated wheat species in general. Since then it is still a matter of discussion.

Timid attempts in the complex consideration of wheat species origin faltered due to the absence of large and representative *Triticum* collections. Only the world wheat collection of the N.I. Vavilov Institute of

Plant Industry (St.-Petersburg, Russia) and the Kyoto Univ. (Kyoto, Japan), have been scrupulously collected and studied sine hundred years. These comprehensive collections are a unique possibility for researchers to look deeper into the *Triticum* phylogeny.

Several wheat domestication schemes suggested in the past do not present our knowledge today. Some of them are misleading or contrarily. On the other hand, modern comparative-genetic and molecular methods might allow us to get deeper insights into phylogenetic relationships within *Triticum* and the related species. The aim of our research was to provide new data to reconstruct the wheat evolution based on chloroplast and nuclear gene loci.

Material and Methods

Plant material

Plants used for chloroplast sequences are indicated in Golovnina et al. (2007). Ten *T. urartu* Thum. ex Gandil. accessions (K-33869, PI 428217, PI 428297, PI 427328, PI 428197, PI 538736, Ig-44829, Ig-45296, Ig-116196, Ig-116198), four *T. boeoticum* Boiss. accessions (K-14384, K-20741, K-25811, K-28300) and 14 *T. monococcum* accessions (K-20970, K-20400, K-18105, KT3-5, G-1777, PI 355517, PI 277137, PI 427927, PI 428175, PI 362610, PI 355523, PI 349049, PI 326317, PI 94743) were used for nuclear sequence analysis. Additional sequence data were obtained from Kilian et al. (2007).

Two *T. antiquorum* Heer ex Udach. accessions K-56397 and K-56398 from Tajikistan and two *T. sphaerococcum* Perciv. accessions K-23790 from India and K-23824 from Pakistan were used for comparative-genetic analyses. The genes determining the compact spike were tested for allelism using the Finnish cultivar Vakka, Buryatian (Russia) accession WAG 8226, and the American accession CI 3090 of *T. compactum* Host.

Total DNA isolation and PCR amplification

Total DNA was isolated from 50–170 mg of fresh leaves using the standard CTAB method (Rogers and Bendich 1985). The primer combinations to amplify the chloroplast *trnT-trnL* intergenic spacer, the *trnL* intron and the *trnK* intron are those described in Golovnina et al. (2006).

In order to amplify A and B genome specific fragments of nuclear DNA, two multiple alignments were developed using sequence data of *Acc1* and *Pgk1* genes (GenBank accession numbers AF343496 - AF343536 and AF343474 – AF343495, respectively, and those from Kilian et al. (2007): DQ290259-DQ290360;DQ290363-DQ290375;DQ364823-DQ364846;DQ290658-DQ290757;DQ290760-DQ290771; DQ364891-DQ364912 for different genomes available among *Triticum* and *Aegilops* L. representatives. Based on these alignments, one pair of B genome specific primers

Acc 3T sense 5'-GCTCATATGGTATATTATGTTCC-3'
 Acc 3T antisense 5'-TTTAGGCACAGAAATAACAT- 3'
 and six different primers for genome A
 AccT1s 5'-GGACTTAGTTTTGTCGTCAAGTT-3',
 AccT1a 5'-GAAAAAAACGCAGGCCAATT-3',
 AccT1a new 5'-CTTCCAAACGTAAGGACCAATACA-3',
 PgkT4s 5'-GCTTGGCTCCCCTGTGCCCG-3',
 PgkT1s new 5'-GGCATTGAGGTATTCTTTGTTCCACTTCCAC-3',
 PgkT1a 5'-CACACTCTCCAGCAGGGATTGCA-3') were designed.

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All PCR reactions were performed in a 20 µl volume containing 65 mM Tris-HCl (pH 8.9), 16 mM (NH₄)₂SO₄, 1.5 mM MgCl₂, 200 µM of each dNTP, 0.5 µM of each primer, 20–50 ng genomic DNA template, and 1 U of *Taq* DNA polymerase. The PCR program had an initial strand separation step at 94°C for 3 min followed by 30 cycles of denaturation at 94°C for 30s, annealing at 42°C for 42s for chloroplast sequences and at 52°C for 42s for nuclear sequence, and elongation at 72°C for 1 min. The PCR products were analyzed in agarose electrophoresis and extracted from gel with a Qiaquick Gel Extraction Kit (Qiagen; according to the manufacturer's protocol).

DNA sequencing and phylogenetic analysis

Two hundred nanograms of the PCR product were used in a 10 µl cycle sequencing reaction with the ABI BigDye Terminator Kit on an ABI 377 DNA sequencer. The nucleotide sequences were aligned using ClustalX software (Thompson et al. 1997) edited using the GenDoc Version 2.6.002 (Nicholas et al. 1997). The phylogenetic tree was generated by the Neighbor-Joining method using MEGA 3.1 program (Kumar et al. 2004). Statistical support for the tree was evaluated by bootstrapping (1000 replications) (Felsenstein 1985).

Results and Discussion

The origin of polyploid wheat species is almost like a “detective story” not all parts are understood so far. Besides, wild diploid (*T. boeoticum* A^bA^b - *T. urartu* A^uA^u) as well as wild tetraploid wheat species *T. dicoccoides* (BBAA) (Körn. ex Aschers. et Graebn.) Schweinf. and *T. araraticum* Jakubz. (GGAA) are morphologically not differentiated from each other and not distinguishable in archeological excavations (Nesbitt 2001). It is further unknown whether the first cultivated naked wheat species in Europe was tetraploid or hexaploid. At the same time, the possibility of their identification is connected with a search of possible wild species involved in cultivated wheat origin and their domestication.

Pile-dwelling wheat

Heer (1865) was the first who described *T. antiquorum* (BBAADD) on the basis of grain remains in archaeological excavations in Switzerland. It is possible that *T. antiquorum* was among the first cultivated hexaploid wheat species in Europe.

T. antiquorum could have played an important role during the early cultivation of hexaploid wheats and it is possible that Asia occupied a central place in this process (Udachin 1992). The drawback of wheat phylogenetic schemes currently proposed consists in the absence of data on the character (type) of genetic control of morphological taxonomically important traits that are identical in their phenotypic manifestation. Since living *T. antiquorum* has been found in Tajikistan (Udachin 1982), it is maybe possible to solve some phylogenetic-related problems for the origin of cultivated hexaploid wheat in Europe. The inheritance of taxonomically important characters was therefore studied in pile-dwelling wheat *T. antiquorum* and two additional contemporary hexaploid wheat species.

These external morphological traits are very often arbitrary. Two basic traits - spherical grains and compact spike – make this wheat distinct from all the other ones.

Spherical grains

Table 1 summarizes the data on the segregation with respect to the grain shape in F₂ hybrids of *T.*

sphaerococcum and *T. antiquorum* accessions and the results of checking the hypothesis that spherical grain genes of these species are allelic. Likewise, no segregation by grain shape was detected in F_2 plants for crosses of K-56397 *T. antiquorum* \times K-23790 *T. sphaerococcum*. Monogenic segregation was observed in F_2 hybrids with common wheat (table 1). This character is controlled monogenically by a recessive gene in K-23790 of *T. sphaerococcum*. Since the character is determined by recessive alleles in both species, F_1 hybrids would express the wild-type (normal) phenotype in the case of non-allelic genes; i.e. the grains would be non-spherical. All 15 grains were spherical in the F_1 hybrid of K-56398 *T. antiquorum* and K-23790 *T. sphaerococcum*. Therefore, the recessive gene determining spherical grain in K-56398 of *T. antiquorum* is allelic to that of K-23790 *T. sphaerococcum*.

Compact spike

The segregations observed in the F_2 hybrids of *T. compactum* cultivar Vakka with accession K-56397 of *T. antiquorum* and accession K-23790 of *T. sphaerococcum* with CI 3090 of *T. compactum* are shown in table 2. The results suggest that the dominant genes, controlling compact spike for *T. compactum* are non-allelic to the genes determining compact spike in *T. antiquorum* and *T. sphaerococcum*. Thus, the relevant *T. antiquorum* and *T. sphaerococcum* genes are different from the dominant *C* gene, which is responsible for compact ear in *T. compactum*.

Table 1. Inheritance of grain shape in F_2 hybrids of hexaploid wheats with *T. antiquorum* and the test for allelic genes controlling spherical grains in *T. antiquorum* and *T. sphaerococcum*, respectively

Cross combination	Number F_2 hybrid plants with grain		χ^2
	spherical	normal	
	1:3	1:15	
triple Dirk D \times <i>T. sphaerococcum</i> K-23790	14	44	0,02
Vrn8 \times <i>T. antiquorum</i> K-56398	18	82	2,61
<i>T. antiquorum</i> K-56397 \times <i>T. sphaerococcum</i> K-23790	238	0	-

Table 2. Inheritance of compact spike in *T. compactum*, *T. sphaerococcum* and *T. antiquorum*

Cross combination	Number F_2 hybrid plants with grain		χ^2
	compact	normal	
	3:1	15:1	
<i>T. compactum</i> Vakka \times <i>T. aestivum</i> K-20900	47	19	0,51
<i>T. compactum</i> Vakka \times <i>T. antiquorum</i> K-56397	79	3	19,92
<i>T. sphaerococcum</i> K-23790 \times <i>T. compactum</i> CI 3090	105	17	7,97

We designated it as *C2*. The origin of the dominant genes *C* and *C2* in hexaploid wheats is unknown because compact spike accessions of *Ae. squarrosa*, the D genome donor of hexaploid wheats, have not been discovered (Goncharov 2002). However, the presence of different non-allelic dominant genes in *T. antiquorum* and *T. compactum* is not indicated a single occurrence of this taxonomically important mutation

in hexaploid wheats. Furthermore, based on the data obtained for non-allelism of genes controlling compact spike in studied hexaploid wheat species, we cannot use the earlier suggested schemes of hexaploid wheat species origin, as non-allelism of genes implies their independent origin. Hence, making up new phylogenetic schemes (for example see Udachin (1982) among others) of wheat origin and new methods are necessary. For this purpose molecular markers for all wheat genomes would be useful in favour to detect and to understand their relationships. Here we provide new sequence data for two chloroplast and two nuclear gene loci.

Chloroplast evidence of wheat evolution

The analysis using all known wheat species including also *Aegilops* species was based on chloroplast *matK* gene comparison along with *trnL* (tRNA - Leu) intron sequences of some species (fig. 1). Based on the neighbor-joining tree, all analyzed wheat and *Aegilops* species are subdivided into four related groups (fig. 1). Polyploid wheat species are divided only into two groups – Emmer I (*T. dicoccoides* and other BBAA *Triticum* species, not shown) and Timopheevii II (*T. araraticum*, *T. timopheevii*, other G genome wheats, and *Ae. speltoides*) dividing B and G genome wheat species. This result corroborates with the previous suggestion of a diphytic origin of polyploid wheats based on earlier hybridological, cytological and molecular analyses (Lilienfeld and Kihara 1934; Mori et al. 1995; Kilian et al. 2007). Group III comprises the diploid AA wheats (*T. boeticum*, *T. monococcum*, *T. urartu*). *Aegilops* section *Sitopsis* and *Vertebrata* members (not shown) and artificial *Aegilotriticum* and *T. palmoniae* are within group IV. Each group I-III includes both wild and cultivated wheat species.

Various *Triticum* and *Aegilops* species were implicated as the donors of genomes of these polyploid wheats (Kerby and Kuspira 1986). Among all the species analyzed for the *Sitopsis* section of *Aegilops* in

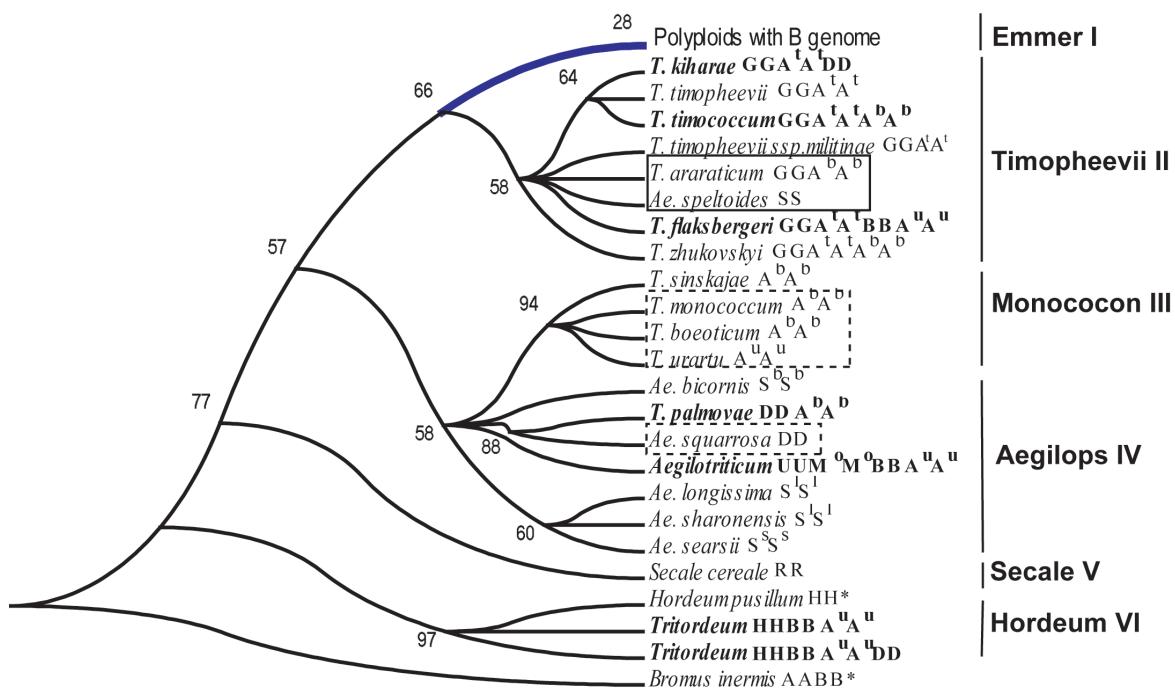


Fig. 1. - Neighbor-Joining phylogenetic tree based on the comparison of *matK* sequences. Four observed clusters are shown by solid lines on the right. The genome composition for each species is indicated. Synthetic wheats are represented in bold letters. For all species belonging to the Emmer group (24 representatives, see table 1 in Golovnina et al. (2007) are indicated as “Polyploids with B genome”. Based on the indel event in the *trnL* intron sequence of some analyzed species, representatives with observed insertions are marked by solid boxes and the rest ones by dotted boxes. Asterisks denote species from which the *matK* sequence was obtained from the GenBank. Bootstrap values are shown.

this study, *Aegilops speltoides* Tausch (included in group II) is most closely related to the polyploid B or G genome. Based on the data presented, both *trnL* and *trnK* intron sequences of *Ae. speltoides* are more variable than the corresponding sequences from all other *Aegilops* and diploid *Triticum* species. Sequences were previously obtained (Golovnina et al. 2007) and submitted in GenBank.

This observation strongly coincides with the previous results based on nucleotide variations of the four other chloroplast non-coding regions and microsatellite repeat motifs (Yamane and Kawahara 2005) and the *ndhF* gene (Kilian et al. 2007). The topology of the trees in both studies clearly demonstrates that the *Ae. speltoides* ancestor branched out before a separation of wild diploid *Triticum* and *Aegilops* species (fig. 1).

Based on our results (Golovnina et al. 2007), it is proposed that one *Ae. speltoides* ancestor was involved the first polyploidization event of wheat species. It is likely that there were two ancestor forms of *Ae. speltoides* involved in a two-step hybridization, i.e. independent events (Emmer and Timopheevii groups). The high degree of intraspecific variation observed among *Ae. speltoides* accessions and differentiation into B and G genome of polyploid wheats support this hypothesis. The G genome and plasmon of the section *Timopheevii* species (clade II) appears evolutionarily younger and is closely related to the contemporary *Ae. speltoides*, whereas the polyploid *Triticum* species (clade I) with the B genome occurred as a result of one more ancient hybridization event with the *Ae. speltoides* ancestor.

Nuclear loci

The presence of four different wheat genomes – A, B, D and G whose various combinations form three groups of *Triticum* species on their ploidy (di-, tetra- and hexaploids) - are well known. The origin of wheat genomes was a matter of discussion since more than seven decades. The A genome is found only in *Triticum* species and is subdivided into two genomes - A^a and A^b, according to the sources of their origin, i.e. two wild diploid wheat species - *T. urartu* and *T. boeoticum*. *T. urartu* was the A genome donor, *Ae. speltoides* was the donor of both B and G genomes, and *Ae. squarrosa* L. (syn.=*Ae. tauschii* Coss.) was that of D genome.

In the present study we have focused our research on the genome A and genome B. We selected two nuclear gene loci *Acc1* and *Pgk1*, because comprehensive datasets were available in gene banks and we provided new data from so far not investigated species.

Total DNA from different *Triticum* and *Aegilops* species has been amplified with A and B genome specific primer combinations. These primers were designed based on unique indels and nucleotide substitutions. The sequencing procedure was conducted with primers complementary to the flanking regions of specificity. The results of PCR analysis of both *Aegilops* and polyploid *Triticum* species completely confirmed the correct choice of primers. The PCR fragments of the expected size have been obtained for homologous genes tested in the samples where the corresponding genomes were present.

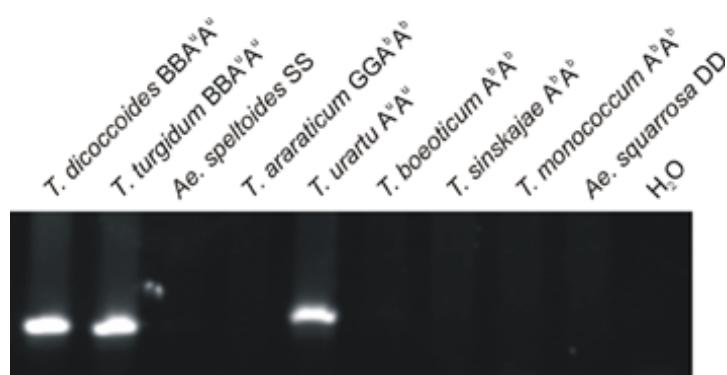


Fig. 2. - PCR amplification with primers Acc 3T sense/Acc 3T antisense which were initially considered to be specific for genome B.

In contrast to the polyploid *Triticum* species, some samples of the diploid A genome wheat species (*T. urartu*, *T. boeoticum* and *T. monococcum*, showed unexpected results. PCR amplification with none A genome specific primers amplified the A genome fragments also successfully, vice versa, PCR amplification with A genome specific primers appeared to be negative. Such results have been obtained for both *Acc1* and *Pgk1* genes. The results of PCR amplification with B genome specific *Acc1* primer combinations are shown in fig. 2.

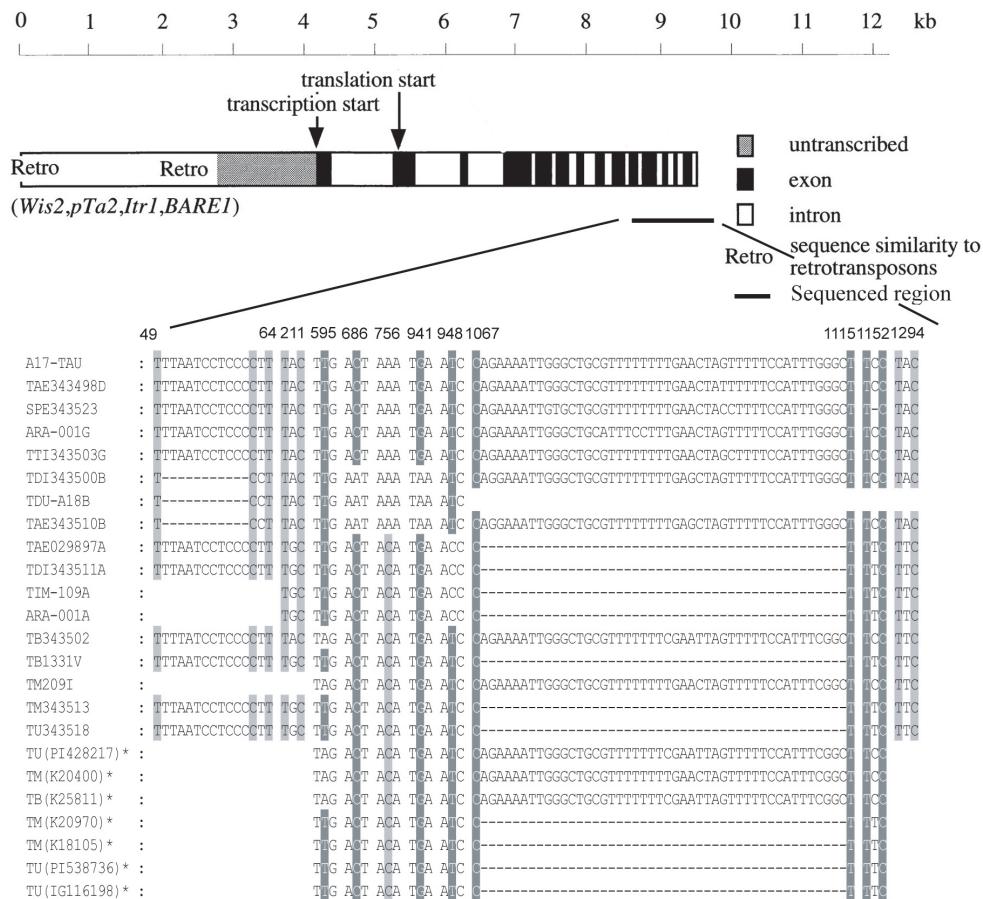


Fig. 3A. - Structure of the plastid *Acc1* gene together with the alignment of the region investigated. Numbers at the top on each column indicate positions in the whole alignment. Asterisks denote sequences obtained in the present study, others were included from Kilian et al. (2007). TAU – *Ae. tauchii*, TAE – *T. aestivum*, SEA – *Ae. searsii*, SPE – *Ae. spelooides*, TIM – *T. timopheevii*, ARA – *T. araraticum*, DIC – *T. dicoccoides*, TDU – *T. durum*, TM – *T. monococcum*, TB – *T. boeoticum*, TU – *T. urartu*. Letters at the end of the sequence name indicate the genome.

In the next step we took a more detailed analysis, focused first on different geographical variants of diploid wheat species of *T. urartu*, *T. boeoticum*, and *T. monococcum*. At the same time, Kilian et al. (2007) published data on *Acc1* and *Pgk1* gene sequences obtained from different wheat species, which were also used for our analysis. The results of these comparative analyses for *Acc1* and *Pgk1* gene sequences are summarized in fig. 3A and fig. 3B.

All analyzed *Acc1* sequences can be divided into two groups due to a 46 bp deletion from position 1067 to position 1151, and some nucleotide substitutions specific for each group (fig. 3A). The first group with the deletion comprises the sequences from polyploid wheat A genomes and also from all three diploid

A genome wheat species. The second group integrates the sequences of *Acc-1* genes from *Ae. speltoides*, those of polyploid wheat B, G, and D genomes and also the sequences of all three diploid A genome *Triticum* species.

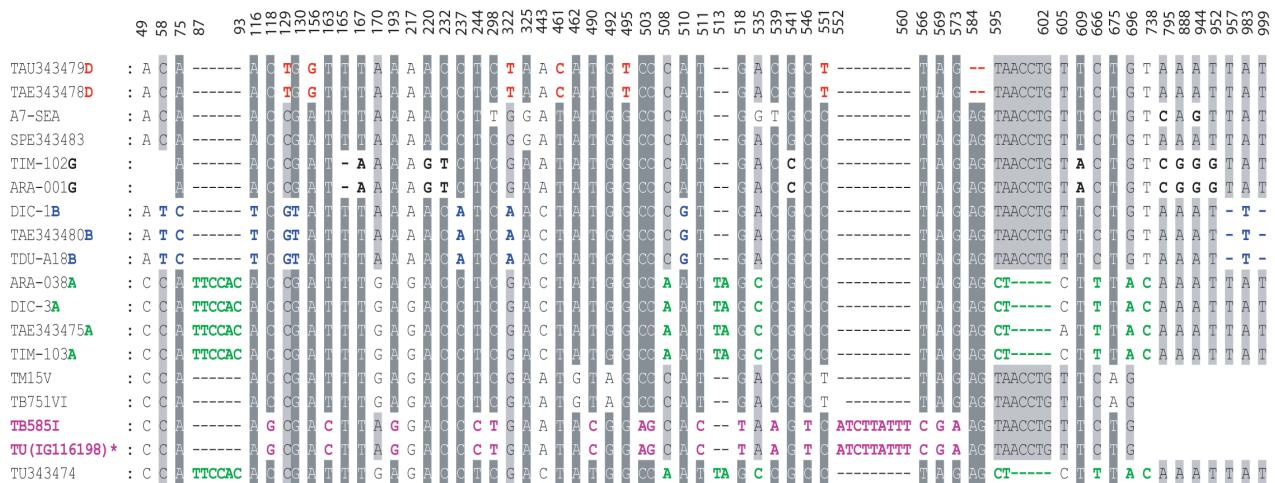


Fig. 3B. - Alignment of the *Pgk1* gene sequences. Only significant invariant sites are shown. Numbers at the top on each column indicate positions in the whole alignment. Genome specific sites or sites specific for diploid species are indicated in bold letters: green – A genome specific, blue - B genome specific, red - D genome specific, black - G genome, purple-specific for two diploid species. Asterisk denotes sequence obtained in the present study, others were used from Kilian et al. (2007). TAU – *Ae. tauchii*, TAE – *T. aestivum*, SEA – *Ae. searsii*, SPE – *Ae. speltoides*, TIM – *T. timopheevii*, ARA – *T. araraticum*, DIC – *T. dicoccoides*, TDU – *T. durum*, TM – *T. monococcum*, TB – *T. boeoticum*, TU – *T. urartu*. Letters at the end of the sequence name indicate the genome.

Thus, diploid A genome wheat sequences are found in both groups. To explain these results, it is necessary to postulate that the wheat genome A originated after the separation of the genus *Triticum* progenitor from the common progenitor with *Aegilops*. Later, both A and B-like A genomes spread among the three diploid wheat species - *T. urartu*, *T. boeoticum* and *T. monococcum* (fig. 4).

The analysis of the *Pgk1* gene sequences is even more phylogenetically informative, and it allows us to divide all the obtained sequences into several groups. First, four groups are definitely outlined in *Pgk1* sequence comparisons according to their position to one of the polyploid wheat genomes A, B, G, or D by the presence of specific indels and specific nucleotide substitutions (fig. 3B). Among the diploid *Triticum* species we have found three different sequences of the *Pgk1* gene fragment. One of these sequences was found in *T. urartu*, which is identical to those from the A genomes of the polyploid wheats. This fact supports that *T. urartu* was the donor of genome A in all polyploid wheats. Two other variants of the *Pgk1* gene were determined in: (I) *T. boeoticum* and *T. monococcum*, and (II) *T. urartu* and *T. boeoticum*, respectively. These sequences are unique and different from the others found in both *Triticum* and *Aegilops* genomes, although the first group (I) is closer to the *Pgk1* gene from *Ae. speltoides*.

Finally, based on the analyses of *Acc-1* and *Pgk1* sequences, we can conclude that three diploid *Triticum* species may contain several different genomes in contrast to the polyploid species in which no heterogeneity has been found. The real significance of these results may be confirmed by genetic experiments for crossing diploid species with different genomes selected in our analysis.

Evolutionary scenario of genus *Triticum*

Based on the comparative and phylogenetic analysis of the chloroplast and nuclear sequences from different *Triticum* and *Aegilops* species obtained in the present study and including published data, we can

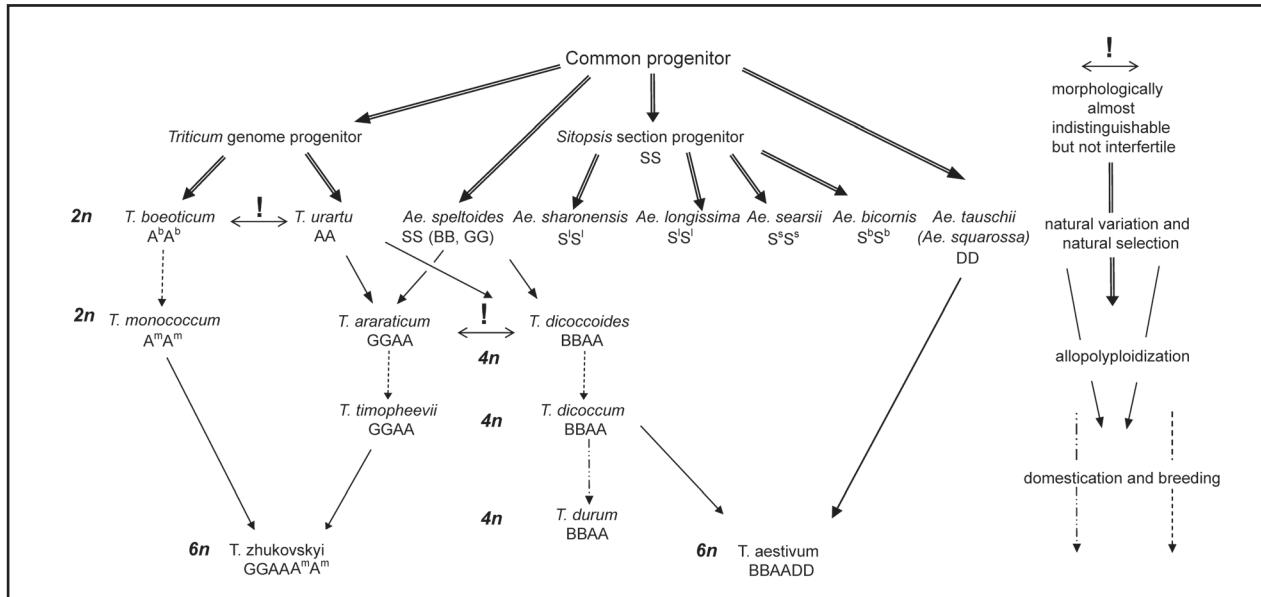


Fig. 4. - Phylogenetic scheme of *Triticum* and *Aegilops* evolution (revised from Kilian et al. 2007).

propose the following evolutionary scenario for genus *Triticum*: I. According to the chloroplast data, we can conclude that *Ae. speltoides* was the donor of the plasmon during polyploid wheat evolution. II. The analysis of nuclear *Acc1* and *Pgk1* gene sequences carried out in this research allows us to hypothesize that a minimum of three different A genome donor lines existed. In contrast, *Ae. speltoides* had only two, which were designated as wheat B and G genomes. III. Interrelations of the three diploid wheat species *T. urartu*, *T. boeoticum* and *T. monococcum* are not well studied, yet. However, it is possible to make some preliminary conclusions. First, it is obvious that wild *T. urartu* was the donor of genome A of all polyploid wheat species, as only in this species the *Pgk1* gene sequence is identical to that of this gene sequence of polyploid wheats. Second, a wild einkorn *T. boeoticum* *Pgk1* haplotype occurs also in cultivated einkorn *T. monococcum*. This supports former findings that *T. monococcum* originated from *T. boeoticum* (Beijerinck 1884; Salamini et al. 2002). Further experiments are still necessary in the future to get deeper insights into the relationships of A genome wheats.

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Chapter 3

Quantification of genetic relationships among A genomes of wheats

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Abstract

The genetic relationships of A-genomes of *Triticum urartu* (A^u) and *Triticum monococcum* (A^m) with polyploid wheats are explored and quantified by AFLP fingerprinting. Forty-one accessions of A-genome diploid wheats, three of AG-genome wheats, 19 of AB, 15 of ABD and one of the D-genome donor *Ae. tauschii* have been analysed. Based on seven AFLP primer combinations, 423 bands were identified as potentially A-genome specific. The bands were reduced to 239 by eliminating those present in autoradiograms of *Ae. tauschii*, bands interpreted as common to all wheat genomes. Neighbour-joining analysis separates *T. urartu* from *T. monococcum*. *T. urartu* has the closest relationship to polyploid wheats. *T. turgidum* ssp *dicoccum* and ssp *durum* lines are included into tightly linked clusters. The hexaploid spelts occupy, in the phylogenetic tree, positions intermediate between bread wheats and *T. turgidum*. The AG-genome accessions cluster in a position quite distant from both diploid and other polyploid wheats. The estimates of similarity between A genomes of diploid and polyploid wheats indicate that, compared to A^m , A^u has around 20% higher similarity to the genomes of polyploid wheats. *T. timopheevii* AG genome is molecularly equidistant from those of A^u and A^m wheats.

Introduction

The genus *Triticum* includes cultivated species cytogenetically associated to four groups: einkorn ($2n=2x=14$, genome AA), emmer ($2n=4x=28$, AABB), *timopheevii* ($2n=4x=28$, AAGG) and bread wheat ($2n=6x=42$, AABBDD) (Sax 1918; Lilienfeld and Kihara 1934; Zohary and Hopf 2000). At the diploid level, two species are recognised: 1) *T. monococcum* L., with a wild form, *T. monococcum* ssp *boeoticum*, a domesticated form, *T. monococcum* ssp *monococcum* and a weedy European form, *T. monococcum* ssp *aegilopoides* (Heun et al. 1997), and 2) *T. urartu* Tum., existing only as a wild form. At the tetraploid level two different groups are distinguished: 1) *T. turgidum* L. with one wild form (*T. turgidum* ssp *dicoccoides* (Korn.)Thell.) and several cultivated subspecies; and 2) *T. timopheevii* Zhuk., with one wild ancestor (*T. timopheevii* ssp *araraticum* (Jakubz.) Mac Key) and one cultivated form (*T. timopheevii* ssp *timopheevii* (Zhuk) Löve and Löve). At the hexaploid level two cultivated species are described: *T. aestivum* L. with several subspecies, and *T. zhukovskyi* Menab. et Ericz.

Origin and phylogenetic relationships of wheat polyploid species have been studied following different approaches. Cytogenetic and morphological studies in the past supported the conclusion that *T. monococcum* was the A-genome donor of polyploid wheats (Sax 1922; Kihara 1924; Lilienfeld and Kihara 1934; Zohary et al. 1969). However, after the recognition of *T. urartu* as a new species, cytogenetic (Chapman et al. 1976), immunochemical (Konarev 1983), electrophoretic (Waines and Payne 1987; Ciaffi et al. 1997) and enzymatic data (Nishikawa 1983) indicated that this species is the most likely progenitor of the A genome of polyploid wheats.

Molecular markers have provided new tools to the study of plant evolutionary relationships: RFLP were used to infer the phylogeny of cultivated wheats, supporting the claim of *T. urartu* as the direct progenitor of polyploid AB and ABD wheats (Dvorak et al. 1988; 1993; Takumi et al. 1993). RFLPs, however, require a large numbers of probe/enzyme combinations to discriminate genotypes and to challenge the genetic relationships of a whole genome. Techniques based on Polymerase Chain Reaction (PCR), on the other hand, are faster, cheaper and less labour-intensive. In particular, AFLP are superior to other markers because of the number of different loci simultaneously analysed per experiment (Powell et al. 1996; Bohn et al.

1998). Relevant is also the capacity of AFLP to fingerprint the whole genome (Heun et al. 1997; Badr et al. 2000; Martin and Salamini 2000) and the possibility of handling a large number of samples per population considered. It is concluded that, when used with appropriate precautions, AFLP fingerprints are informative also for phylogenetic studies (Buntjer et al. 2002).

To quantify the molecular differences among the A genomes of diploid and polyploid wheats is important: the possibility of creating chimaeric recombinant A^m and A^u chromosomes (unpublished results from our laboratories) is worthwhile only if the two genomes differ substantially. We have applied the AFLP procedure to a large sample of *Triticum* species in order to quantify the level of similarity of A^m and A^u genomes to those of AB, AG and ABD polyploids.

Methods

Plant material

The 41 A-genome (37 A^m and four A^u), three AG-genome, 19 AB-genome, 15 ABD-genome and one D-genome wheats listed in table 1 were provided by several genebanks (see acknowledgment). The 37 A^m diploid lines were chosen among a group of 338 accessions fingerprinted by Heun et al. (1997) and representative of a wider pool of 1362 accessions morphologically characterised (Empilli 1994). The four A^u lines were chosen among a group of more than 100 lines of *T. urartu*, based on maximisation of their genetic distance evaluated by AFLP (data not shown).

DNA isolation and AFLP procedures

DNA from 30 seven-day-old seedlings per accession was extracted following a modified CTAB procedure (Murray and Thompson 1980); AFLP analysis was performed as described by Vos et al. (1995). Briefly, DNAs were digested with *Eco*RI + *Mse*I, then adapter sequences were ligated to the restricted DNA fragments. PCR was performed in two consecutive steps. In the first, the selective pre-amplification, DNAs were amplified with primers complementary to the adapters and having one selective nucleotide, *Eco*RI primer +A and *Mse*I primer +A. In the second step, the preamplification products were used as template for amplification using primers with the following extensions: E-ACC+M-ACC, E-ACG+M-AGC, E-ACG+M-ATT, E-AGC+M-ACT, E-AGT+M-AAC, E-AGT+M-ACA and E-AGT+M-ACT. For these reactions, only the *Eco*RI primer was labelled with [³³P]ATP (Amersham). PCR products were separated by electrophoresis in a 4.5% denaturing polyacrylamide gel and visualised by autoradiography.

Data analysis

For each genotype, the presence (1) or the absence (0) of amplified fragments was recorded. Two consecutive steps were adopted to select A-genome specific bands in polyploids: in the first step, only bands comigrating with diploid *T. monococcum* and *T. urartu* fragments were kept; in the second step all bands comigrating with D-genome *Ae. tauschii* fragments were eliminated. The reason to consider the diploid *Ae. tauschii* was that its D genome is different from diploid A genomes. This situation allows to spot AFLP bands which, due to the existing homoeology among A, B and D genomes, are common to all diploid and polyploidy wheats, while not mapping uniquely to A chromosomes. In the absence of clear indications concerning diploid B and G genome donors, the second step was restricted to *Ae. tauschii*. The correct attribution of AFLP bands to the A genome was tested by fingerprinting few representative diploid wheats along with Chinese Spring and its nulli-A-tetrasomics. A restricted set of primer combination was used

Table 1. Accessions considered in the quantification of the A-genome relationships among wheats

	Species	Origin	Passport
A^m			
ID68	<i>T. monococcum</i> ssp <i>boeoticum</i>		PRG6150
ID126	<i>T. monococcum</i> ssp <i>boeoticum</i>		HTRI6734/89
ID229	<i>T. monococcum</i> ssp <i>boeoticum</i>		BGRC36551
ID386	<i>T. monococcum</i> ssp <i>boeoticum</i>	Turkey	G1878
ID521	<i>T. monococcum</i> ssp <i>boeoticum</i>	Hungary	PI272556
ID604	<i>T. monococcum</i> ssp <i>boeoticum</i>	Turkey	PI427470
ID618	<i>T. monococcum</i> ssp <i>boeoticum</i>	Turkey	PI427484
ID746	<i>T. monococcum</i> ssp <i>boeoticum</i>	Turkey	PI427614
ID758	<i>T. monococcum</i> ssp <i>boeoticum</i>	Turkey	PI427627
ID909	<i>T. monococcum</i> ssp <i>boeoticum</i>	Iraq	PI427782
ID1075	<i>T. monococcum</i> ssp <i>boeoticum</i>	Iraq	PI427949
ID1089	<i>T. monococcum</i> ssp <i>boeoticum</i>	Turkey	PI427963
ID1117	<i>T. monococcum</i> ssp <i>boeoticum</i>	Lebanon	PI427995
ID1121	<i>T. monococcum</i> ssp <i>boeoticum</i>	Lebanon	PI427999
ID1174	<i>T. monococcum</i> ssp <i>boeoticum</i>	Turkey	PI538540
ID1182	<i>T. monococcum</i> ssp <i>boeoticum</i>	Iraq	PI538548
ID1256	<i>T. monococcum</i> ssp <i>boeoticum</i>	Turkey	PI538623
ID1261	<i>T. monococcum</i> ssp <i>boeoticum</i>	Turkey	PI538723
ID1303	<i>T. monococcum</i> ssp <i>boeoticum</i>	Turkey	PI554540
ID1310	<i>T. monococcum</i> ssp <i>boeoticum</i>	Turkey	PI554550
ID1315	<i>T. monococcum</i> ssp <i>boeoticum</i>	Turkey	PI 554559
ID1326	<i>T. monococcum</i> ssp <i>boeoticum</i>	Turkey	PI554577
SAL1366	<i>T. monococcum</i> ssp <i>boeoticum</i>	Armenia	
ID69	<i>T. monococcum</i> ssp <i>monococcum</i>	Turkey	G4325
ID127	<i>T. monococcum</i> ssp <i>monococcum</i>	Turkey	AT12910/89
ID194	<i>T. monococcum</i> ssp <i>monococcum</i>	Austria	BGRC13193
ID279	<i>T. monococcum</i> ssp <i>monococcum</i>	Balkans	BGRC42016
ID409	<i>T. monococcum</i> ssp <i>monococcum</i>	Turkey	16273
ID494	<i>T. monococcum</i> ssp <i>monococcum</i>	Turkey	PI167526
ID495	<i>T. monococcum</i> ssp <i>monococcum</i>	Turkey	PI167589
ID500	<i>T. monococcum</i> ssp <i>monococcum</i>	Turkey	PI167634
ID576	<i>T. monococcum</i> ssp <i>monococcum</i>	Israel	PI393496
ID1157	<i>T. monococcum</i> ssp <i>monococcum</i>	Spain	PI518452
ID26	<i>T. monococcum</i> ssp <i>aegilopoides</i>	Rumania	PI306532
ID123	<i>T. monococcum</i> ssp <i>aegilopoides</i>		ASchgt1/88
ID228	<i>T. monococcum</i> ssp <i>aegilopoides</i>	Balkans	BGRC36548
ID520	<i>T. monococcum</i> ssp <i>aegilopoides</i>	Hungary	PI272520
A^u			
ID388	<i>T. urartu</i>	Lebanon	G3246
ID1122	<i>T. urartu</i>	Lebanon	PI428000
ID1264	<i>T. urartu</i>	Turkey	PI554479
ID1277	<i>T. urartu</i>	Turkey	PI554498
AG (+AAG)			
ID1233	<i>T. timopheevii</i> ssp <i>araraticum</i>	Iraq	PI538599
FAR72	<i>T. timopheevii</i> ssp <i>timopheevii</i>		W899
FAR77	<i>T. zhukowskyi</i>	Georgia	ATRI7262/74
AB hulled			
TD10	<i>T. turgidum</i> ssp <i>dicoccum</i>	Italy	
TD15	<i>T. turgidum</i> ssp <i>dicoccum</i>	Italy	
TD33	<i>T. turgidum</i> ssp <i>dicoccum</i>	Italy	
TD47	<i>T. turgidum</i> ssp <i>dicoccum</i>	Italy	

AB naked

Aristan	<i>T. turgidum</i> ssp <i>durum</i>	France
Aziziah	<i>T. turgidum</i> ssp <i>durum</i>	Italy/Palestine
Cappelli	<i>T. turgidum</i> ssp <i>durum</i>	Italy/Tunisia
Coll. Jordan	<i>T. turgidum</i> ssp <i>durum</i>	Jordan
Muri S 503	<i>T. turgidum</i> ssp <i>durum</i>	Cyprus
Razza	<i>T. turgidum</i> ssp <i>durum</i>	Tunisia
Roqueño	<i>T. turgidum</i> ssp <i>durum</i>	Spain
Sabil 1	<i>T. turgidum</i> ssp <i>durum</i>	Syria
Santa	<i>T. turgidum</i> ssp <i>durum</i>	Greece
Taganrog	<i>T. turgidum</i> ssp <i>durum</i>	Ukraina
Timilia	<i>T. turgidum</i> ssp <i>durum</i>	Italy
Tripolino	<i>T. turgidum</i> ssp <i>durum</i>	Italy
Vatan	<i>T. turgidum</i> ssp <i>durum</i>	Tajikistan
Villemure	<i>T. turgidum</i> ssp <i>durum</i>	France
TT3243	<i>T. turgidum</i> ssp <i>polonicum</i>	

ABD hulled

TS24	<i>T. aestivum</i> ssp <i>spelta</i>	Italy
TS58	<i>T. aestivum</i> ssp <i>spelta</i>	Italy
TSRouquin	<i>T. aestivum</i> ssp <i>spelta</i>	Germany
TSTrivento	<i>T. aestivum</i> ssp <i>spelta</i>	Italy

ABD naked

Chinese spring	<i>T. aestivum</i> ssp <i>aestivum</i>	China
Akagomugi	<i>T. aestivum</i> ssp <i>aestivum</i>	Japan
Daruma 2	<i>T. aestivum</i> ssp <i>aestivum</i>	Japan
Gabo	<i>T. aestivum</i> ssp <i>aestivum</i>	Australia
Hatif Inversable	<i>T. aestivum</i> ssp <i>aestivum</i>	France
Red Egyptian	<i>T. aestivum</i> ssp <i>aestivum</i>	Africa
Rieti	<i>T. aestivum</i> ssp <i>aestivum</i>	Italy
Squarehead master	<i>T. aestivum</i> ssp <i>aestivum</i>	England
Wilhelmina	<i>T. aestivum</i> ssp <i>aestivum</i>	Holland
TA3238	<i>T. aestivum</i> ssp <i>compactum</i>	
TA3240	<i>T. aestivum</i> ssp <i>macha</i>	

D

ID1608	<i>Ae. tauschii</i>	Iran
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(the nullitetrasicomic N2AT2B in this experiment was missing). The results of this control, although partial, supported band assignments carried out in the two steps mentioned above.

Similarities between pair-wise accessions were estimated by the Dice similarity index (Dice 1945): $S_{Dxy} = n_{xy}/(n_{xy} + u_{xy}/2)$, where n_{xy} represents the number of bands common to two accessions x and y and u_{xy} is the number of bands present only in x or only in y. A dendrogram based on the similarity matrix data was generated using Neighbour Joining (NJ) and the goodness of the tree was tested by bootstrapping (1000 runs). This analysis was performed with the softwares DistAFLP (Mougel et al. 2002) and Phylip version 3.6 (Felsenstein 2002).

Consensus genotypes for each species and for each subspecies were obtained by scoring as 0 gene frequencies up to 0.5 and the remainder as 1; Dice genetic similarities were computed using consensus values and two trees, one reporting species and the other sub-species relationships, were built by NJ. Similarly, genetic distances based on the frequency of each band in each group were computed using Nei's (1972) distance with the software AFLP-SURV1.0 (Vekemans 2002) and NJ clustering performed. Bootstrap testings (1000 runs) were performed as outlined.

Results

Molecular profiling of the 79 *Triticum* accessions with seven primer pair combinations yielded 738 polymorphisms (AFLP bands present or absent). During the evaluation of AFLP markers across species, criteria were followed to assign a band to homoeologous loci, as described by El Rabey et al. (2002). Primer combinations differed widely in their ability to amplify polymorphic products: the average number of AFLP polymorphisms per gel was 105, ranging from 55 (E-AGT + M-AAC) to 163 (E-ACG + M-ATT).

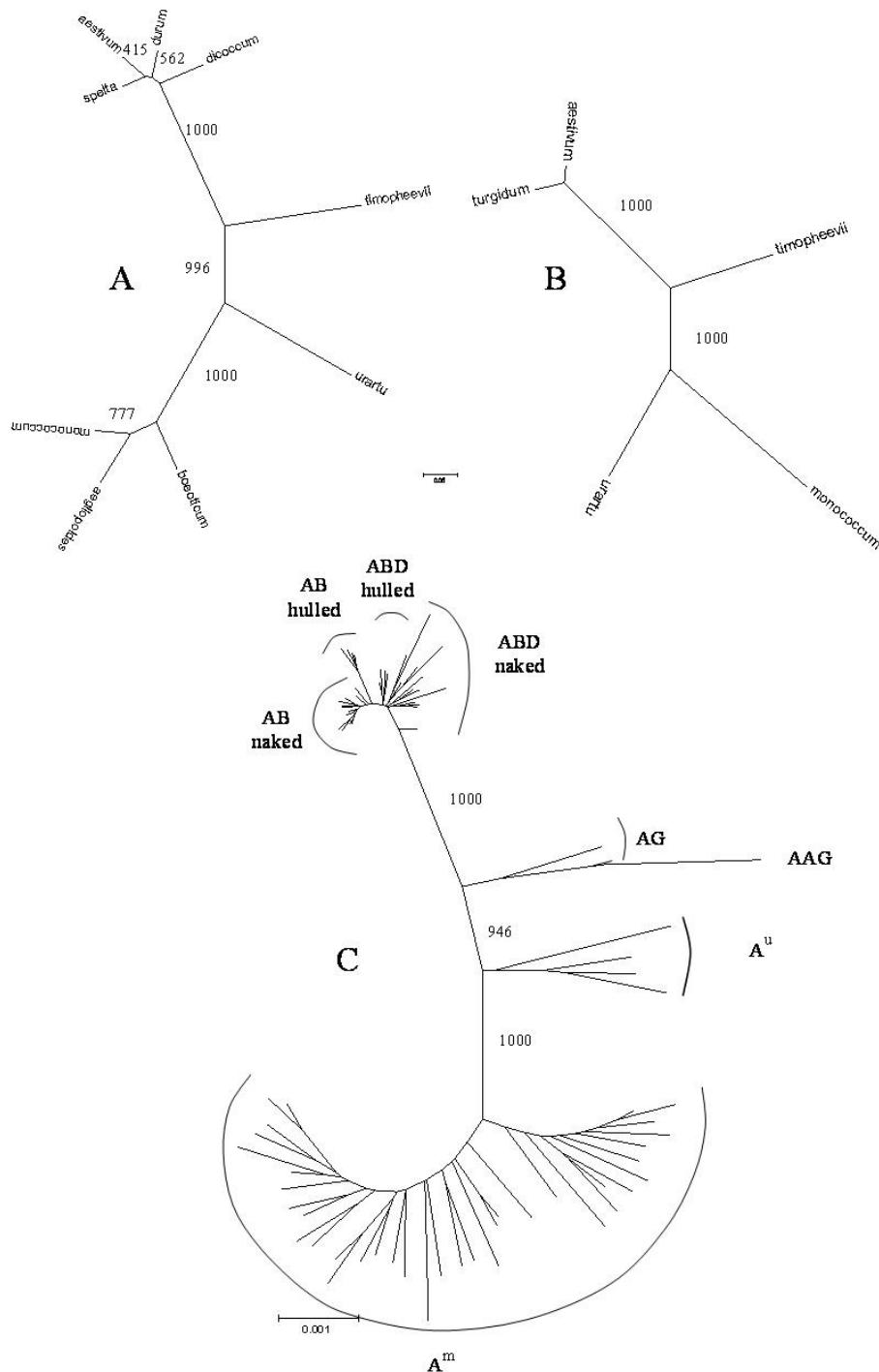


Fig. 1. - Neighbour-joining tree of Dice genetic similarities. Bootstrap consensus values from 1000 iterations are indicated. 239 AFLP bands related to genome A were considered (specified in Materials and Methods). In A and B, the consensus genotypes were obtained by scoring as 0 gene frequencies up to 0.5 and the remainder as 1; in C, topologies from all accessions studied are reported.

Table 2. Dice genetic similarities among genome A accessions and polyploid wheats, based on 239 AFLP bands (see Materials and Methods)

Genome A line	4n wheats (AB)	6n wheats (ABD)	4n Timopheevii (AG+AAG)	
<i>Triticum monococcum</i> ssp <i>boeoticum</i>				
ID68	0.365 ± 0.0034	0.363 ± 0.0065	0.510 ±	0.0191**
ID126	0.404 ± 0.0023	0.411 ± 0.0047	0.427 ±	0.0082
ID229	0.394 ± 0.0033	0.410 ± 0.0048	0.473 ±	0.0185
ID386	0.364 ± 0.0029	0.372 ± 0.0045	0.477 ±	0.0182
ID521	0.408 ± 0.0024	0.406 ± 0.0030	0.451 ±	0.0272
ID604	0.386 ± 0.0024	0.374 ± 0.0053	0.458 ±	0.0195
ID618	0.349 ± 0.0029	0.354 ± 0.0045	0.457 ±	0.0196
ID746	0.322 ± 0.0032*	0.330 ± 0.0046*	0.457 ±	0.0123
ID758	0.363 ± 0.0028	0.355 ± 0.0038	0.437 ±	0.0109
ID909	0.382 ± 0.0031	0.384 ± 0.0045	0.483 ±	0.0180
ID1075	0.381 ± 0.0027	0.370 ± 0.0052	0.502 ±	0.0101
ID1089	0.398 ± 0.0038	0.402 ± 0.0054	0.482 ±	0.0221
ID1117	0.345 ± 0.0040	0.362 ± 0.0059	0.454 ±	0.0149
ID1121	0.365 ± 0.0026	0.382 ± 0.0057	0.458 ±	0.0089
ID1174	0.355 ± 0.0026	0.364 ± 0.0057	0.426 ±	0.0023*
ID1182	0.372 ± 0.0035	0.379 ± 0.0050	0.494 ±	0.0171
ID1256	0.422 ± 0.0032	0.445 ± 0.0037**	0.496 ±	0.0074
ID1261	0.376 ± 0.0045	0.387 ± 0.0038	0.486 ±	0.0171
ID1302	0.426 ± 0.0023**	0.436 ± 0.0041	0.491 ±	0.0207
ID1310	0.423 ± 0.0021	0.424 ± 0.0043	0.502 ±	0.0172
ID1315	0.395 ± 0.0030	0.407 ± 0.0047	0.475 ±	0.0188
ID1326	0.408 ± 0.0030	0.422 ± 0.0059	0.477 ±	0.0104
SAL1366	0.386 ± 0.0024	0.384 ± 0.0058	0.478 ±	0.0212
<i>Triticum monococcum</i> ssp <i>monococcum</i>				
ID69	0.330 ± 0.0024	0.339 ± 0.0046	0.439 ±	0.0164
ID127	0.330 ± 0.0024	0.339 ± 0.0046	0.439 ±	0.0164
ID194	0.405 ± 0.0026	0.412 ± 0.0049	0.467 ±	0.0111
ID279	0.350 ± 0.0038	0.353 ± 0.0039	0.419 ±	0.0100*
ID409	0.325 ± 0.0025*	0.335 ± 0.0036*	0.421 ±	0.0176
ID494	0.396 ± 0.0022	0.407 ± 0.0038	0.481 ±	0.0155
ID495	0.385 ± 0.0019	0.383 ± 0.0040	0.483 ±	0.0165**
ID500	0.371 ± 0.0028	0.378 ± 0.0038	0.453 ±	0.0121
ID576	0.393 ± 0.0026	0.403 ± 0.0037	0.475 ±	0.0058
ID1157	0.425 ± 0.0027**	0.431 ± 0.0050**	0.479 ±	0.0139
<i>Triticum monococcum</i> ssp <i>aegilopoides</i>				
ID26	0.348 ± 0.0024	0.359 ± 0.0044	0.429 ±	0.0154
ID123	0.329 ± 0.0029	0.334 ± 0.0042	0.395 ±	0.0195
ID228	0.318 ± 0.0023*	0.328 ± 0.0038*	0.393 ±	0.0112*
ID520	0.387 ± 0.0025**	0.399 ± 0.0040**	0.444 ±	0.0211**
<i>Triticum urartu</i>				
ID388	0.489 ± 0.0024*	0.477 ± 0.0053*	0.473 ±	0.0225*
ID1122	0.507 ± 0.0032**	0.508 ± 0.0049	0.524 ±	0.0306**
ID1264	0.503 ± 0.0039	0.509 ± 0.0046**	0.521 ±	0.0266
ID1277	0.495 ± 0.0026	0.480 ± 0.0066	0.495 ±	0.0203

(*: within group lowest similarity; **: within group highest similarity).

Considering as comparison the diploid A-genome wheats, 423 polymorphic loci were identified as hosting putative A-bands. Fragments comigrating with D-genome bands of the *Ae. tauschii* accession were subsequently deleted. This process yielded 239 putative A-bands complying with the conditions described, and these were retained for further analysis. A comparison of Chinese Spring and its nulli-A tetrasomics with representative diploids mapped 33 of 63 putative A-bands on A chromosomes. This fraction of 52.4% supports the assignment of our AFLP bands to the A genome, given that Chinese Spring was characterized only by 67.6% of the bands present across hexaploid lines studied.

The wheat accessions grouped following the well-known wheat taxonomy (fig. 1C). All the A^m-genome samples (*T. monococcum*) clustered together, separated from A^u diploids (*T. urartu*). At the polyploids level, the two AG- and the AAG-genome accessions clustered in a small group distant from both diploids and other polyploids. The AB tetraploids formed one group, divided into two strictly related sub-groups: the four *T. turgidum dicoccum* formed the first one, while all the 14 *T. turgidum durum* made up the second; the accession of *T. turgidum polonicum* mapped alone. The hexaploid group was represented by two subgroups, the first containing all bread wheats and the second including the spelt, these fitting between 4n and 6n wheats.

Table 3. Average values of Dice genetic similarities (\pm s.e.) among diploid and polyploid wheats

Species	N°	Dice genetic similarity ^a				
		4	15	4	11	3
		AB (hulled)	AB (naked)	ABD (hulled)	ABD (naked)	AG + AAG
<i>T. monococcum</i> (wild)	23	0.39 \pm 0.003	0.38 \pm 0.002	0.39 \pm 0.003	0.39 \pm 0.002	0.47 \pm 0.004
<i>T. monococcum</i> (domest)	10	0.38 \pm 0.005	0.37 \pm 0.003	0.38 \pm 0.006	0.38 \pm 0.004	0.46 \pm 0.006
<i>T. monococcum</i> (feral)	4	0.35 \pm 0.005	0.35 \pm 0.004	0.35 \pm 0.008	0.36 \pm 0.005	0.42 \pm 0.010
A ^m genome	37	0.38 \pm 0.003	0.37 \pm 0.001	0.38 \pm 0.003	0.38 \pm 0.002	0.46 \pm 0.004
A ^u genome (<i>T. urartu</i>)	4	0.50 \pm 0.004	0.50 \pm 0.002	0.50 \pm 0.003	0.49 \pm 0.005	0.50 \pm 0.012

Note: Two hundred thirty-nine AFLP bands related to genome A are considered (specified in Materials and Methods). N° of lines;

^aSimilarity varies between 0 and 1 (maximum).

The dendrograms based on consensus genotypes (see Materials and Methods) showed a similar picture (fig. 1A and fig. 1B), with a high level of confidence for most branches; only the relationships between *T. dicoccum* and *T. durum*, as well as *T. aestivum* and *T. spelta*, showed intermediate values. Similar results were observed using Nei (1972) genetic distances based on AFLP fragments frequencies (data not shown).

The values of Dice genetic similarity for genome A among diploid and polyploid wheats are presented in table 2. All *T. urartu* samples, compared to any *T. monococcum* spp accession, showed a closer relationship with the AB and ABD genome wheats. The same clear-cut result was not observed when the *T. timopheevii* group was considered: in this case, ranges of *T. urartu* and *T. monococcum* accessions overlapped partially. These observations are synthesized in table 3, reporting the average values of Dice genetic similarities between diploid and polyploid wheats: while the closer relationship between *T. urartu* and AB and ABD wheat accessions is unmistakable, AG wheats show roughly the same similarity with A^m and A^u diploids.

Our estimate of the genetic similarity between genomes A^m and A^u, on one side, and polyploids AB and ABD on the other, indicate that A^u has around 20% higher similarity with A genomes of polyploids.

However, *T. timopheevii* (genome AG) appears to be almost molecularly equidistant from A^u and A^m, a finding which may indicate that the G genome is more similar to A genomes than previously thought.

Average values of A-genome genetic similarities recorded for single accessions of wheats revealed different from 3.6 to 25.8% (values with asterisk in table 2). This finding highlights the necessity, when similar types of analyses are carried out, of using a congruous number of accessions.

Discussion

The quest for the donor of genome A to the polyploid wheats was settled in the last 20 years based on different approaches (Chapman et al. 1976; Konarev 1983; Waines and Payne 1987; Nishikawa 1983), including those based on molecular markers (Dvorak et al. 1988, 1993; Takumi et al. 1993). The available results indicate that *T. urartu* is the genome A progenitor of polyploid wheats, a case of paternal contribution (Provan et al. 2004).

On the other hand, several studies indicate a high level of similarity between the chromosomes of *T. monococcum* and of *T. aestivum* (Dubcovski et al. 1995; Luo et al. 2000), suggesting that A^u and A^m genomes, notwithstanding their high sterility when crossed, have not diverged very significantly since their separation from a common progenitor. A quantification of their difference, however, has not yet been provided.

AFLPs are a reliable and powerful method for the detection of DNA polymorphisms because they are well reproducible, show a high multiplex ratio (Powell et al. 1996) and allow a genome-wide scanning of genetic variation (Heun et al. 1997; Badr et al. 2000). This is not the case of sequence-based studies that are limited to restricted genome regions having mutation rates that may vary widely.

AFLPs have been included among “discontinuous” DNA markers (Martin and Salamini 2000): they describe variations of a DNA sequence scattered along the genome while, when gene sequences are compared, the nucleotides considered are contiguous. The capacity of AFLP to portray nucleotide variation is well recognised (Innan et al. 1999; Mougel et al. 2002), and they provide a measure of π , the genomic nucleotide diversity index of Nei and Li (1979). In this paper AFLP markers were exploited to assess the differences existing among A genomes of diploid A^m and A^u wheats and their polyploid relatives. In this context, a drawback of AFLPs is the existence of fragment length homoplasy, i.e. the comigration of non-homologous fragments. In barley, it has been demonstrated that different genotypes have comigrating AFLP bands derived from orthologous DNA sequences. In the same *Hordeum* genus, more caution has to be used in interspecific comparisons, but the same criterium can be adopted (Badr et al. 2000). In *Triticum* species, the A, B, D and G genomes derive from a common ancestor and, being molecularly similar, they may share the same AFLP bands. This situation raises questions on genome assignment of specific AFLPs.

To elucidate and quantify the relationship between the genomes of diploid and polyploid wheats, only A-bands are useful, given that the B genome is common to tetraploid and hexaploid species, and the D genome is present only in hexaploid wheats. *T. urartu* and *T. monococcum* have, by definition, only AFLP A-bands. The problem arises when polyploid wheats must be fingerprinted and the search is restricted to AFLP A-bands. In such a case, our approach to identify specific A-bands involved two steps: a) in polyploid wheats, only bands comigrating with those of diploid A wheats were considered; b) bands comigrating with those of the *Ae. tauschii* were discarded as a way to minimize identical-by-descent fragments homoplasies. This procedure reduced the original 423 polymorphic bands, observed in *T. monococcum* and *T. urartu* as well as in the polyploids, to 239 putative A-bands. As a final control, the correct classification of the putative A-bands of Chinese Spring was assessed by comparison with its nulli-A-tetrasomics. The results showed that

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53% of the Chinese Spring bands were related to the A genome, a satisfactory value considering that only 67% of putative AFLP A bands in our set of hexaploid lines were present in Chinese Spring.

Our results demonstrate that the A^u genome of *T. urartu* is more similar by around 20% to the A genome of AB and ABD wheats, compared to the A^m genome of *T. monococcum*. This difference is much smaller when the comparison with the AG genome of *T. timopheevii* is considered. As evident from fig. 1C, the estimate is not affected by the pooling of the hexaploid *T. zhukovskyi* (A^uA^mG genome) with the tetraploid AG wheats. The comparable similarity existing between the genome A of the two diploids and the same genome of the *T. timopheevii* group might be due to the mode of origin of this last species. Our finding, as a matter of fact, supports the hypothesis that the G genome is more similar, as previously thought, to A genomes.

The AFLP-based phylogenetic tree obtained from the putative A-bands is consistent with the cytotaxonomical data on species relationships in the genus *Triticum*. *T. urartu* and *T. monococcum* ssp *boeoticum* are sympatric diploid wheats, with a geographical distribution partially overlapping that of wild tetraploids. Accessions of the two species were first discriminated by seed protein electrophoretic pattern and based on few morphological characters (Johnson and Dhaliwal 1976). Since its recognition, *T. urartu* has been suggested as the donor of the A-genome to the polyploid wheats. Our results support the today obvious conclusion that *T. urartu* and *T. monococcum* are indeed different species. That the A-genome of polyploid wheats derives from *T. urartu*, and that only a limited part of the broad variation existing in the diploid genepool is present in the polyploid wheats, are accessory, confirmatory results of our study.

The two AG and one AAG genome accessions group far from all the other species. *T. timopheevii* and *T. zhukovskyi* wheats are still cultivated in a limited Caucasus area. Probably they are the result of a limited number of hybridisations generating small gene pools. Unpublished results of our laboratory show, as previously suggested (Zohary and Hopf 2000), that AG domesticated wheats derive from *T. araraticum*, but fail to prove where geographically this event has taken place. This leaves some uncertainties on the putative donor of the G genome, because of the missing correlation between the geographical distribution of putative wild donors and a sample of domesticated accessions. Measures of genomic similarity provided in this paper open the discussion on a testable hypothesis: does *T. araraticum* derive from interspecific crosses between *T. boeoticum* and *T. urartu*?

Triticum aestivum ssp *spelta*, considered the transition form to naked hexaploid wheats (Mc Fadden and Sears 1946), has been later reported to have a more recent appearance in fossil records. In our phylogenetic trees this wheat has a topology intermediate between hexaploid and tetraploid wheats. Molecular fingerprinting of spelts from Italy and Germany strengthens the hypothesis of Liu and Tsunewaki (1991) and Dvorak and Luo (2001), which propose the introgression of non-free-threshing emmer genes into *T. aestivum* ssp *aestivum* as the most likely origin of European spelts.

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CHAPTER 3

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Chapter 4

Independent wheat B and G genome origins in outcrossing *Aegilops* progenitor haplotypes

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Abstract

The origin of modern wheats involved allopoloidization among related genomes. To determine if *Aegilops speltoides* was the donor of the B and G genomes in AABB and AAGG tetraploids, we used a 3-tiered approach. Using 70 amplified fragment length polymorphism (AFLP) loci, we 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 *Triticum aestivum* wheat lines. 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 *ACCI*, *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 AABB *Triticum dicoccoides* and AAGG *Triticum araraticum* lineages during their independent origins.

Introduction

Bread wheat, *Triticum aestivum*, has no direct hexaploid wild progenitor (Morris and Sears 1967; Kimber and Feldman 1987). The species possesses 3 sets of homologous chromosomes, designated as AABBDD, whose origins have differing degrees of certainty. The D chromosomes stem from the wild diploid *Aegilops tauschii* (Kihara 1944) through allopoloidization with the wild AABB tetraploid *Triticum dicoccoides*. The A and B chromosomes of that tetraploid derive from an earlier hybridization between the wild AA diploid *Triticum urartu* (Dvorak et al. 1993) and a wild diploid B genome donor: the ultimate source of this B genome is still discussed. A related conundrum is the origin of AAGG *Triticum araraticum*, whose A genome also stems from *T. urartu*, whereby the wild G progenitor is frequently reported to be *Aegilops speltoides* (Rodriguez, Maestra et al. 2000). The B donor is traditionally sought in the Sitopsis section of the genus *Aegilops* (Sarkar and Stebbins 1956; Kerby and Kuspira 1988). Previous molecular analyses of single-gene loci for a few accessions are not inconsistent with the view that both the B genome of *T. dicoccoides* (AABB) and the G genome of *T. araraticum* (AAGG) might trace to the Sitopsis section, in genetic proximity to wild *Ae. speltoides* (Blake et al. 1999; Rodriguez, Maestra et al. 2000; Zhang et al. 2002). However, there are caveats.

First, nuclear and cytoplasmically inherited markers yield contrasting results on the issue of B genome origin (discussed in Wang et al. 1997). In addition, ancient allelic diversity among wild ancestors, compounded by the possibility of unrecognized hybridization events, renders inferences of the B progenitor questionable (Huang et al. 2002) in the absence of genome-wide surveys for many loci and accessions. Furthermore, the outcrossing nature of *Ae. speltoides* (Kimber and Feldman 1987) renders introgression for individual loci difficult to exclude in the absence of extensive lineage sampling. Importantly, cytogenetic evidence does not support the view that *Ae. speltoides* was the donor of B or G genome, even though such suggestions can be found (Maestra and Naranjo 1998). When synthetic SSAA genomes (S contributed by *Ae. speltoides* and A by *Triticum*) are crossed to *Triticum durum* (AABB, the domesticated form of *T. dicoccoides*), sterility is observed, pointing to differences between S and B genomes; the same is reported for S and G genomes (Dvorak 1972; Kimber and Athwal 1972). Moreover, B–S pairing in wheat/*Ae. speltoides*

hybrids is comparable to that noted for wheat/*Aegilops longissima* and wheat/*Aegilops sharonensis* hybrids (Fernandez-Calvin and Orellana 1994), suggesting that B chromosomes of polyploid wheats do not pair preferentially to those of *Ae. speltoides*.

Understanding hexaploid wheat origin would further its genetic improvement (Salamini et al. 2002; Chantret et al. 2005). Here, we report a comprehensive amplified fragment length polymorphism (AFLP) survey of genomic diversity among 1372 individuals from 480 wild B genome progenitor candidates. Through the analysis of Sears's (1954) nulli–tetrasomic (AADD) lines, B genome–specific AFLPs were identified. For ~70 domesticated and progenitor lines representing the breadth of wild genomic diversity, haplotypes at nuclear loci *ACCI*, *G6PDH*, *GPT*, *PGK1*, *Q*, *VRN1* and of the chloroplast locus *ndhF* were determined. Comparisons to haplotypes from AA *Triticum boeoticum*, *Triticum monococcum*, and *T. urartu* identified haplotypes specific to the B genome to allow comparison to Sitopsis accessions. The data circumscribe molecular diversity among Sitopsis *Aegilops* species and specify the nature of wheat B and G genome origins.

Methods

AFLP Analysis

The 480 *Aegilops* lines used in this study are listed in Supplementary table S1. DNA was isolated from freeze-dried or silica-dried leaves of 1372 plants (Supplementary table S2), using the Qiagen (Hilden) DNeasy Kit, and amplified as described by Zabeau and Vos (1993) using the primer combinations E^{ACC}/M^{ACA}, E^{ACC}/M^{AGC}, and E^{ACC}/M^{AGG}. The AFLP bands were scored as 1 or 0 (present or absent). Jaccard (1908) similarities of the 850 individuals with different AFLP patterns (Supplementary table S3) were computed using DistAFLP (Mougel et al. 2002), and Neighbor-Joining (NJ) bootstrap trees were inferred with PHYLIP 3.6 (Felsenstein 2002). DNA from 94 selected *Aegilops*, *T. boeoticum*, *T. urartu*, *T. dicoccoides*, *T. araraticum*, and *T. aestivum* accessions (Supplementary table S4), along with *T. aestivum* Chinese Spring aneuploids: 6 nulliB–tetraD (N1BT1D, N2BT2D, N3BT3D, N4BT4D, N5BT5D, N6BT6D) and 5 nulliB–tetraA (N1BT1A, N2BT2A, N3BT3A, N5BT5A, N7BT7A) (Sears 1954), was amplified using primer combinations E^{ACC}/M^{AGC}, E^{ACC}/M^{AGG}, E^{ACG}/M^{ACC}, E^{ACG}/M^{ACT}, E^{ACG}/M^{AGG}, E^{ACG}/M^{AGT}, E^{AGC}/M^{AGC}, and E^{AGC}/M^{ATA}. NeighborNet (NNet) planar graphs (Bryant and Moulton 2004) of AFLP Hamming distances between individuals were constructed with SplitsTree 4.1 (Huson and Bryant 2006).

Haplotype Analysis

Genes and accessions considered for haplotype analysis are recorded in Supplementary tables S5–S7. Sixty-seven lines were common to all loci—*T. dicoccoides* (34), *T. dicoccum* (5), *T. durum* (1), *T. araraticum* (5), *T. timopheevii* (6), *Ae. bicornis* (2), *Ae. longissima* (2), *Ae. searsii* (2), *Ae. sharonensis* (2), *Ae. speltoides* (7), and *Ae. tauschii* (1). Other sequences from additional lines of those same species, from *T. boeoticum*, *T. monococcum*, *T. urartu*, *T. araraticum*, and *T. timopheevii* (table 2), as well as available published sequences were included. DNA was isolated as described above. Primers (Supplementary table S8) were designed with Primer3 against sequences for *ACCI* (Huang et al. 2002), *G6PDH* (Nemoto et al. 1999), *GPT* (GenBank AF548741), *PGK1* (Huang et al. 2002), *Q* (Faris et al. 2003), *VRN1* (Sherman et al. 2004; Yan et al. 2004), and *ndhF* (Ogihara et al. 2002). Some accessions of *Ae. speltoides* have 2 copies each of the genes *ACCI* and *PGK1* (Huang et al. 2002); primers for these 2 genes were used allowing the amplification of the same gene in all *Ae. speltoides*. DNA amplifications were performed in 25 µl containing ~100 ng of leaf DNA,

0.4 µM of each primer, 125 µM of each deoxynucleoside triphosphate (AB gene, Surrey, UK), 3 mM MgCl₂, 4% dimethyl sulfoxide, and 1 unit of *Taq* DNA polymerase incubated in a PTC-225 Tetrad Thermal Cycler (MJ Research) as follows: 94 °C for 3 min, 28–33 cycles of 30 s at 94 °C, 20–40 s at 59–65 °C, 50–95 s at 72 °C, and a final extension step of 6 min at 72 °C. Polymerase chain reaction products were sequenced on both strands (Supplementary table S9, Supplementary Material online). Sequences (Supplementary table S10) were processed with Applied Biosystems DNA Sequencing Analysis Software 5.1.1 and manually inspected with BioEdit version 7.0.1 (Hall 1999). The alignments were generated with ClustalW, and the haplotypes were scored manually and with DnaSP (Rozas et al. 2003). For homozygous loci, only one haplotype per line was included in the alignment, both haplotypes for heterozygous loci. Median-joining (MJ) networks (Bandelt et al. 1999) were constructed with the Network 4.1.1.2 program (Fluxus Technology Ltd, Clare, Suffolk, UK). Total number of substitutions per site between populations, Da (equation 10.21; Nei 1987), using the Jukes–Cantor method was calculated with DnaSP (Rozas et al. 2003).

To obtain A, B, and G genome–specific haplotype sequences for polyploid wheats, three approaches were used. When B genome–specific sequence differences were available, 1) primer combinations were designed and used for haplotype-specific amplification and sequencing; 2) amplification products from A, B, and G genomes were obtained with the A genome primers, but sequenced using genome-specific primers; and 3) in the remaining cases, amplification products for A, B, and G genomes were obtained using nondiscriminating A genome primers, cloned in *Escherichia coli*, and at least 3 sequences per clone obtained, until both haplotypes were identified by comparison to existing A and B genome data for the locus.

Results

Genomic Diversity within the Sitopsis Section of *Aegilops*

To survey the molecular diversity among candidate B genome donors, we studied 2–3 plants each from a total of 501 accessions spanning all 5 *Sitopsis Aegilops* species—*Ae. searsii*, *Ae. bicornis*, *Ae. sharonensis*, *Ae. longissima*, and *Ae. speltoides*—collected along the Eastern Mediterranean (fig. 1). (We follow Dorofeev et al. [1979] for *Triticum* binomial nomenclature and Van Slageren [1994] for *Aegilops*). Accessions were grown in 2003 and morphologically reidentified, whereby 21 misassigned lines or interspecific hybrids were discarded. DNA was collected from 1372 plants: *Ae. bicornis* (39 accessions, 105 individuals), *Ae. longissima* (81, 227), *Ae. searsii* (97, 285), *Ae. sharonensis* (112, 327), *Ae. speltoides* (149, 422) and from the D genome outgroup species *Ae. tauschii* (2, 6).

A screen using 3 AFLP primer combinations uncovered a total of 70 polymorphic bands across all plants. This revealed 850 individuals with different AFLP patterns: *Ae. bicornis* (36 accessions, 44 individuals), *Ae. longissima* (80, 165), *Ae. searsii* (54, 77), *Ae. sharonensis* (101, 176), *Ae. speltoides* (147, 386), and *Ae. tauschii* (2, 2). The NJ tree of Jaccard (1908) distances is shown in figure 2 and provides an overview of *Sitopsis* genome diversity. The primary screen revealed the breadth of divergence within each species, helping to choose accessions for subsequent fine-scale analyses. In addition, two notable results emerged. First, in all intraspecific pairwise comparisons, AFLP-based genetic similarity was lower in the outbreeder *Ae. speltoides* than in any of the other members of the section which are inbreeders (Kimber and Feldman 1987) (fig. 2). Second, figure 2 shows that the *Sitopsis* section (with one exception, a plant of *Ae. bicornis* mapping outside but near the major cluster of the species) does not include other genetically distinct major groups, besides those represented by *Ae. bicornis*, *Ae. searsii*, *Ae. speltoides*, and the *Ae. sharonensis*–*Ae. longissima* cluster (the two last species, however, mapped to some degree separately when using more AFLP

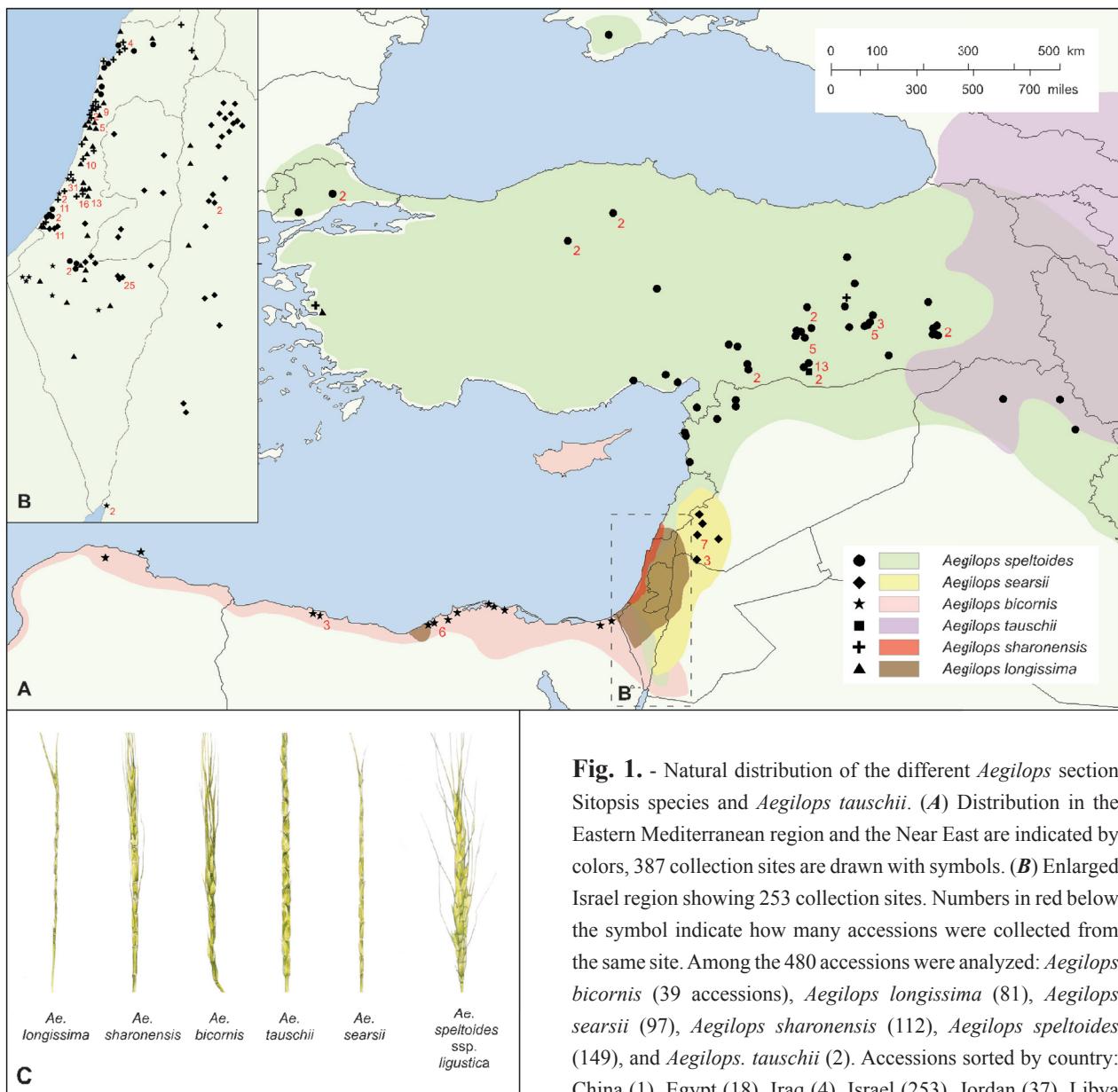


Fig. 1. - Natural distribution of the different *Aegilops* section *Sitopsis* species and *Aegilops tauschii*. (A) Distribution in the Eastern Mediterranean region and the Near East are indicated by colors, 387 collection sites are drawn with symbols. (B) Enlarged Israel region showing 253 collection sites. Numbers in red below the symbol indicate how many accessions were collected from the same site. Among the 480 accessions were analyzed: *Aegilops bicornis* (39 accessions), *Aegilops longissima* (81), *Aegilops searsii* (97), *Aegilops sharonensis* (112), *Aegilops speltoides* (149), and *Aegilops tauschii* (2). Accessions sorted by country: China (1), Egypt (18), Iraq (4), Israel (253), Jordan (37), Libya (2), Portugal (2), Syria (29), Turkey (70), and Ukraine (1), 63

analyzed accessions of unknown origin are not shown in the figure. *Aegilops* species sorted by country: China (1 SPE), Egypt (18 BIC), Iraq (4 SPE), Israel (9 BIC, 69 LOG, 52 SEA, 104 SHA, 20 SPE), Jordan (4 BIC, 5 LOG, 28 SEA), Libya (2 BIC); Portugal (2 SPE), Syria (16 SEA, 13 SPE), Turkey (1 LOG, 2 SHA, 64 SPE, 2 TAU), Ukraine (1 SPE), and unknown (6 BIC, 6 LOG, 1 SEA, 6 SHA, 44 SPE). Country known, but exact collection site unknown within the country 27 (Israel: 3 LOG, 3 SHA, 1 SPE; Jordan: 2 BIC, 2 LOG, 6 SEA; Syria: 2 SEA, 7 SPE; Turkey: 1 SPE). (C) Spike morphologies for *Aegilops* species relevant to this study.

primer combinations, like in fig. 3A and B). It is concluded that the *Sitopsis* section does not contain cryptic species molecularly distinct from those currently recognized (Kimber and Feldman 1987), such that our sample appears to span the full breadth and depth of molecular diversity within the section. The inability to distinguish *Ae. sharonensis* from *Ae. longissima* individuals in the coarse screen is irrelevant here, as are the low bootstrap proportions for branches separating species at these 70 loci.

Higher Resolution among Wild and Domesticated Genomes

A reduced set of 59 *Aegilops* plants representative for molecular diversity within the section was considered for further AFLP studies, carried out with a higher number of primer combinations. The selected

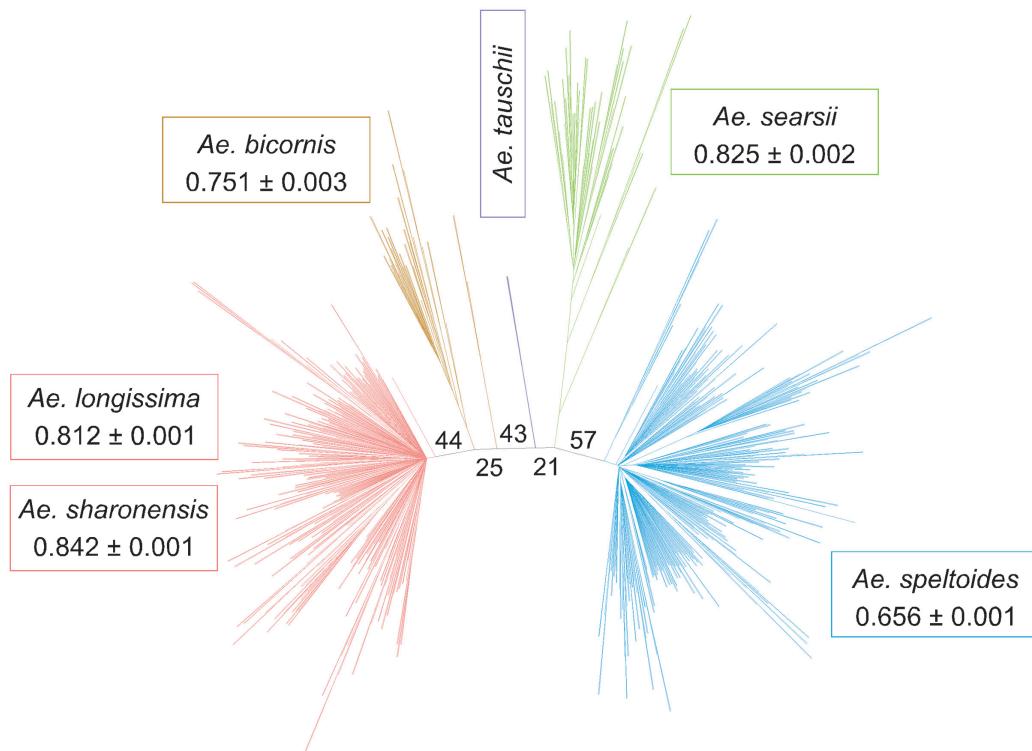


Fig. 2. - Unrooted NJ tree of Jaccard (1908) distances based on AFLP markers describing genetic relationships among 850 individuals of the genus *Aegilops*, section *Sitopsis*, and *Aegilops tauschii*. The 850 genotypes—*Aegilops bicornis* (36 accessions, 44 individuals), *Aegilops longissima* (80, 165), *Aegilops searsii* (54, 77), *Aegilops sharonensis* (101, 176), *Aegilops speltoides* (147, 386), and *Ae. tauschii* (2, 2)—were selected as unique pattern out of a total of 1372 one-plant samples. A total of 70 AFLP polymorphic loci were generated with primer combinations E36M35, E36M40, and E36M41. Bootstrap proportions for the main internal edges are shown. Numbers within boxes report the average intraspecific value of Jaccard (1908) genetic similarity (\pm standard error).

plants were *Ae. bicornis* (11 individuals), *Ae. longissima* (8), *Ae. searsii* (13), *Ae. sharonensis* (13), and *Ae. speltoides* (14). Selection of plants within species was carried out, maximizing the average genetic distances among selected plants. Two plants from the *Ae. tauschii* (D genome) outgroup were included, as were 5 *T. aestivum* cultivars (AABBDD), 3 wild *T. dicoccoides* (AABB), 4 wild *T. araraticum* (AAGG, the progenitor of the domesticated *T. timopheevii*), 9 wild *T. boeoticum* (A^bA^b , the progenitor of the domesticated *T. monococcum*, A^mA^m), and 12 wild *T. urartu* (AA). The choice of the 9 and 12 accessions, respectively, of *T. boeoticum* and *T. urartu* considered the criterion specified above, based on published and unpublished molecular data of the authors. Other *Triticum* accessions were chosen as representative of molecular diversity among the species considered in experiments previously published by the authors (references in Salamini et al. 2002).

Eleven AFLP primer combinations amplified 375 polymorphic bands across these 94 lines, from which NNet splits graphs can be interpreted like trees in that they contain splits (branches) with weights (lengths). Parallel lines identify the same split or branch. Boxes indicate support for 2 competing patterns of taxon relationship. NNet splits graphs highlight the predominant phylogenetic signals in the data and the extent to which these signals may or may not be tree-like (Huson and Bryant 2006). In cases of reticulate evolutionary history, hybrid taxa are suggested by the occurrence of incompatible splits (which appear as boxes), often with hybrid taxa being linked by splits to their potential parents. NNet split graphs only display the contradictory splits that can be visualized in a single plane and should not be considered an explicit model of reticulate evolutionary history. Nevertheless, they provide an implicit

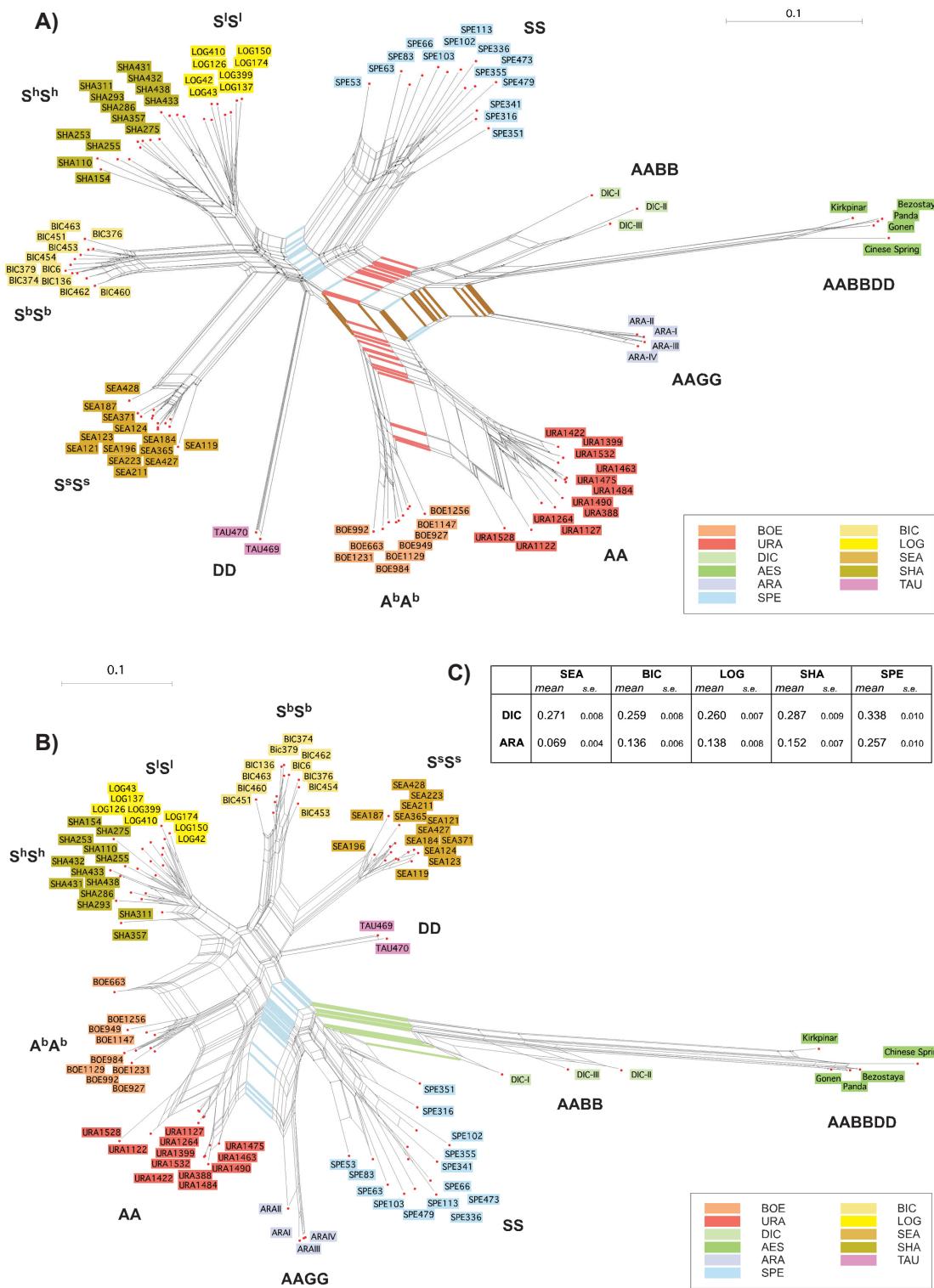


Fig. 3. - NNets of Hamming distances for AFLP polymorphisms among *Sitopsis* section, *Aegilops* species, and *Aegilops tauschii* (outgroup) with polyploid wheats. **(A)** NNet for 375 polymorphic loci (11 AFLP primer combinations) and 94 lines. AES, *Triticum aestivum*; ARA, *Triticum araraticum*; BIC, *Aegilops bicornis*; BOE, *Triticum boeticum*; DIC, *Triticum dicoccoides*; LOG, *Aegilops longissima*; SEA, *Aegilops searsii*; SHA, *Aegilops sharonensis*; SPE, *Aegilops speltoides*; TAU, *Aegilops tauschii*; and URA, *Triticum urartu*. The number of individuals considered was 5 (AES), 4 (ARA), 11 (BIC), 9 (BOE), 3 (DIC), 8 (LOG), 13 (SEA), 13 (SHA), 14 (SPE), 2 (TAU), and 12 (URA). Genome assignments are shown. Relevant splits are highlighted (see text). **(B)** NNets based on 65 AFLP polymorphic loci (11 primer combinations) assigned specifically to B chromosomes of *T. aestivum* using Chinese Spring nulli-tetrasomic lines for the same 94 lines. Other details as in **(A)**. **(C)** Jaccard (1908) genetic similarity index (average proportion of identical B genome-specific AFLP bands) among *T. dicoccoides* (DIC)/*T. araraticum* (ARA) lines and *Aegilops* species based on the 65 AFLP B bands in **(B)**.

representation of evolutionary history (Huson and Bryant 2006) and one that is useful for identifying and exploring different signals and their meaning. For allopolyploid species, NNet has an advantage for data visualization over tree-building methods, which assume that the data have evolved on a single bifurcating tree. At this level of genome-wide comparison, the only Sitopsis member that shared a split with the AABB, AAGG, and AABBDD polyploids was *Ae. speltoides*. That split reflects a higher proportion of shared AFLP bands between polyploid wheats and *Ae. speltoides* as compared with other SS genomes. A second split divides *T. urartu* (AA) from all diploids sampled but excludes *T. boeticum* (A^bA^b), and indeed *T. urartu* is the A genome donor (Dvorak et al. 1993). No split links *Ae. tauschii* (DD) to the hexaploid AABBDD genome. However, this might be expected because the NNet method can only represent incompatible splits projected onto 2 dimensions (Huson and Bryant 2006). With the D genome absent in the 7 tetraploids sampled, signals from A, B, G, and S genomes will override the weaker signal linking AABBDD and DD genomes. A strong split linking the AA diploids with *T. araraticum* (AAGG) to the exclusion of *T. dicoccoides* (AABB) is also observed, indicating that the AABB and AAGG genomes, both involving *T. urartu*, are the result of independent polyploidization events.

The B Genome

Six nulliB–tetraD and 5 nulliB–tetraA lines of the hexaploid cultivar Chinese Spring (Sears 1954) were included in the AFLP analysis. They identified 65 bands that reside specifically on the B genome. If the split that links *Ae. speltoides* to polyploids is a historical component of genome similarity, it should become more prominent in the NNet based on the 65 B genome–specific bands. This is observed in figure 3B, where the split linking *Ae. speltoides* to polyploid wheats is highlighted in blue. These B bands were selected by virtue of their occurrence in hexaploid wheat, not by virtue of their character state among tetraploids or diploids. Hence, they do not skew the locus sample systematically toward any potential B genome donor. They represent B genome–specific signals with regard to polyploid origins; competing A- and D-specific signals are diminished, but not abolished, because A, B, G, and D genomes are still related at these loci.

Figure 3B reveals that the *Ae. speltoides* genome is most similar to the B and G genomes of polyploid wheats. And because we have extensively sampled genome diversity across the Sitopsis (fig. 2), this indicates that the *Ae. speltoides* S genome is the extant version of B and G genomes of polyploid wheats. Identical B genome–specific AFLP bands shared between tetraploid wheats and the species of the Sitopsis section using the Jaccard (1908) similarity (fig. 3C) further support that conclusion.

The NNet shows a strong split linking hexaploid wheat with *T. dicoccoides* to the exclusion of *T. araraticum*, highlighted in green in figure 3B. This corresponds to the well-known participation of *T. dicoccoides* in bread wheat origin (Dvorak et al. 1993). Evidence for additional hybridization events was uncovered, namely the strong component of similarity linking few *T. urartu* (AA) accessions to the *T. boeticum* complex (A^bA^b), probably reflecting interspecific crosses. However, even in the B genome–specific data, no *Ae. speltoides* genome sampled was specifically more similar to all polyploids sampled. Nonetheless, if the B and G genomes stem from within *Ae. speltoides*, then genome-specific haplotypes from polyploids should provide more detailed evidence for that origin.

Congruent Evidence from Haplotypes

Haplotypes recognized in DNA fragments for the nuclear genes *ACCI*, *G6PDH*, *GPT*, *PGK1*, *Q*, and *VRN1* and in a 719-bp region of the chloroplast gene *ndhF* were determined for tetraploids, Sitopsis members, and AA diploids. In total, 0.73 Mb of sequence data were obtained and combined with 80,000 bp from previous studies (Supplementary tables S5–S7, Supplementary Material online) for analysis. At all

Table 1. Sequence divergence between tetraploid wheat and *Sitopsis* section haplotypes (boldface: divergence between S and B or G genomes)

Gene (<i>L</i>) ^b	Genome (<i>n</i>)	<i>D_a</i> ± SE × 10 ³ (<i>n</i>) ^a in comparison with				
		<i>Ae. bicornis</i>	<i>Ae. longissima</i>	<i>Ae. searsii</i>	<i>Ae. sharonensis</i>	<i>Ae. speltoides</i>
<i>ACCI</i> (366)	dicA ^c (37)	14 ± 2 (3)	12 ± 2 (5)	17 ± 2 (6)	14 ± 2 (4)	5 ± 1 (23)
	dicB ^d (37)	14 ± 2 (3)	12 ± 2 (5)	17 ± 2 (6)	14 ± 3 (4)	5 ± 1 (23)
	araA ^e (5)	14 ± 5 (3)	12 ± 4 (5)	17 ± 4 (6)	14 ± 5 (4)	5 ± 1 (23)
	araG ^f (6)	10 ± 5 (3)	8 ± 5 (5)	13 ± 5 (6)	10 ± 5 (4)	1 ± 2 (23)
<i>G6PDH</i> (537)	dicA (34)	54 ± 8 (2)	53 ± 8 (2)	51 ± 8 (2)	53 ± 8 (2)	43 ± 4 (15)
	dicB (34)	52 ± 8 (2)	52 ± 8 (2)	50 ± 8 (2)	52 ± 8 (2)	12 ± 3 (15)
	araA (5)	52 ± 19 (2)	52 ± 19 (2)	50 ± 18 (2)	52 ± 19 (2)	39 ± 8 (15)
	araG (6)	48 ± 18 (2)	48 ± 18 (2)	46 ± 17 (2)	48 ± 18 (2)	10 ± 4 (15)
<i>GPT</i> (673)	dicA (34)	9 ± 1 (2)	14 ± 2 (2)	9 ± 1 (2)	14 ± 2 (2)	21 ± 2 (7)
	dicB (34)	15 ± 2 (2)	17 ± 3 (2)	15 ± 2 (2)	17 ± 3 (2)	3 ± 0.3 (7)
	araA (5)	9 ± 3 (2)	13 ± 5 (2)	9 ± 3 (2)	14 ± 5 (2)	20 ± 4 (7)
	araG (5)	15 ± 6 (2)	17 ± 6 (2)	15 ± 6 (2)	17 ± 6 (2)	0 ± 0.4 (7)
<i>PGK1</i> (665)	dicA (35)	24 ± 5 (2)	21 ± 3 (2)	26 ± 4 (2)	21 ± 3 (2)	12 ± 2 (16)
	dicB (35)	24 ± 5 (2)	19 ± 3 (2)	24 ± 4 (2)	21 ± 3 (2)	15 ± 4 (16)
	araA (5)	24 ± 10 (2)	21 ± 7 (2)	26 ± 10 (2)	21 ± 7 (2)	12 ± 4 (16)
	araG (5)	19 ± 9 (2)	16 ± 6 (2)	19 ± 7 (2)	16 ± 6 (2)	15 ± 5 (16)
<i>Q</i> (917)	dicA (36)	111 ± 16 (2)	81 ± 14 (3)	100 ± 15 (2)	94 ± 16 (3)	68 ± 6 (13)
	dicB (36)	77 ± 11 (2)	48 ± 11 (3)	85 ± 12 (2)	55 ± 13 (3)	20 ± 3 (13)
	araA (5)	113 ± 41 (2)	83 ± 32 (3)	102 ± 37 (2)	96 ± 35 (3)	70 ± 14 (13)
	araG (5)	65 ± 24 (2)	35 ± 18 (3)	75 ± 28 (2)	43 ± 20 (3)	12 ± 5 (13)
<i>VRNI</i> (304)	dicA (34)	53 ± 8 (2)	53 ± 8 (2)	56 ± 8 (2)	53 ± 8 (2)	58 ± 5 (11)
	dicB (34)	28 ± 4 (2)	28 ± 4 (2)	35 ± 5 (2)	28 ± 4 (2)	26 ± 3 (11)
	araA (5)	53 ± 19 (2)	54 ± 19 (2)	57 ± 21 (2)	53 ± 19 (2)	58 ± 11 (11)
	araG (5)	20 ± 7 (2)	21 ± 7 (2)	28 ± 10 (2)	20 ± 7 (2)	19 ± 5 (11)
<i>ndhF</i> (719)	dic-cp ^g (34)	6 ± 1 (2)	6 ± 1 (2)	6 ± 1 (2)	6 ± 1 (2)	0 ± 0.2 (7)
	ara-cp (9)	6 ± 2 (2)	6 ± 2 (2)	6 ± 1 (2)	6 ± 1 (2)	0 ± 0.3 (7)

^a total number of substitutions per site between populations ± SE (Nei 1987) calculated with DnaSP (Rozas et al. 2003);^b *n*: number of loci sequenced for each species^c *T. dicoccoides* A genome^d *T. dicoccoides* B genome^e *T. araraticum* A genome^f *T. araraticum* G genome^g chloroplast genome

nuclear loci investigated, the number of net nucleotide substitutions per site between populations (Nei 1987), *Da*, revealed that *T. dicoccoides* B genome haplotypes were always more similar to those in *Ae. speltoides* than those in any other species. The same was true for comparisons of the *T. araraticum* G genome haplotypes (table 1), providing additional evidence for an origin of both B and G genomes from a *Ae. speltoides* donor. The same was evident for the cytoplasmically inherited *ndhF* gene (table 1).

MJ networks for these loci (fig. 4) reveal higher levels of haplotype diversity within the outbreeder *Ae. speltoides* than in other wheats. Furthermore, B and G genome haplotypes of the tetraploids were consistently more closely related to *Ae. speltoides* than to other sources. At *G6PDH*, 8 *Ae. speltoides* haplotypes were observed: SPE-I is the closest relative of B and G haplotypes, which are monomorphic for *T. dicoccoides* and dimorphic for *T. araraticum*, whereas other *Sitopsis* or A genome haplotypes are distinct by ≥20 substitutions. At *ACCI*, *Ae. speltoides* revealed 7 haplotypes: SPE-I and -II are identical to those found in G genome,

SPE-III is the closest relative of the major *T. dicoccoides* B haplotype; no *ACCI* haplotypes are shared between *Ae. speltoides* and remaining Sitopsis species. A genome haplotypes at *ACCI* were much less diverse than B genome homologues. At *GPT*, only one *Ae. speltoides* haplotype was observed, which is identical to the major *T. araraticum* haplotype and shows only 2 nucleotide differences to the main *T. dicoccoides* B haplotype; other Sitopsis or A genome haplotypes were clearly distinct. *Q* was by far the most polymorphic locus sampled: the closest progenitor to the main *T. dicoccoides* B genome haplotype was SPE-I, different by 7 nucleotides to the *T. araraticum* haplotype and by 17 nucleotides from the major *T. dicoccoides* B haplotype; the other haplotypes were more distant to B and G genomes. At *PGK1*, 13 *Ae. speltoides* haplotypes were found: SPE-I differed by 2 nucleotides from the main B haplotype of *T. dicoccoides*; the rare SPE-II is not more closely related to the single *T. araraticum* G haplotype than haplotypes found among other Sitopsis; for this gene, a greater diversity of *Ae. speltoides* haplotypes relative to other Sitopsis was particularly evident. *VRN1* (Supplementary fig. S1, Supplementary Material online) did not reveal a closer relationship for either *Ae. speltoides* or other Sitopsis to B or G genome. For this gene, the simplest interpretation is that our present lineage sample at *VRN1* did not uncover *Ae. speltoides* B genome progenitor haplotypes: only a clear distinction between A and B/G genome-specific haplotypes was evident.

The main *Ae. speltoides* *ndhF* haplotype was identical with that of tetraploids and hexaploids (fig. 4). The network, while excluding the progenitors of *Ae. bicornis*, *Ae. longissima*, *Ae. sharonensis*, and *Ae. searsii* as the B female recipients in the cross with the A genome, provides evidence that female gametes of *Ae. speltoides* generated the AABB and AAGG genomes.

In summary, the MJ networks uncover no Sitopsis haplotypes that are more similar to B or G genome than *Ae. speltoides* haplotypes are, indicating that the *Ae. speltoides* gene pool participated in the synthesis of AABB and AAGG genomes. Furthermore, loci that are highly polymorphic in *Ae. speltoides*, such as *PGK1*, underscore the need to sample many lineages to uncover B genome progenitor alleles.

The 2 distinct G genome haplotypes at *ACCI* differing by 4 substitutions, each identical to haplotypes occurring in *Ae. speltoides*, could, at face value, suggest 2 independent origins for *T. araraticum*. However, for all loci at which the B genome donor was heterozygous—for instance, in unreduced gametes—both alleles should persist in modern tetraploids. This problem is related to the outcrossing nature of *Ae. speltoides* (table 2): of the 39 loci investigated, 76% were heterozygous as compared with 7.4% for remaining *Aegilops* species, all predominantly inbreeders (Kimber and Feldman 1987). The distinctness of B and G genome haplotypes at all nuclear loci, and the proximity of *Ae. speltoides* progenitors in most cases, clearly indicates independent alloplodization events underlying *T. araraticum* and *T. dicoccoides* origins, consistent with their divergent positions in the analysis of B genome-specific AFLPs (fig. 3B). The results of table 3, which underscore the close relationship of B and G genomes relative to A genome, support this conclusion.

Discussion

Domestication of wheats commenced about 10 000 years ago (Salamini et al. 2002), but the events that gave rise to wild polyploids are older. Estimates for the age of *T. dicoccoides* origin range from >0.5 MYA (Huang et al. 2002), 0.25–1.3 MYA (Mori et al. 1995; Huang et al. 2002), or 0.36 MYA (Dvorak and Akhunov 2005) but are heavily subject to haplotype sampling variance, as our data underscore, for which reason the B genome donor has remained in issue. Though the source of the B genome has been sought among Sitopsis (Sarkar and Stebbins 1956; Kerby and Kuspira 1988), with a focus on *Ae. speltoides* (Dvorak and Zhang 1990; Huang et al. 2002), genetic data have been equivocal (Dvorak 1972; Kimber and Athwal

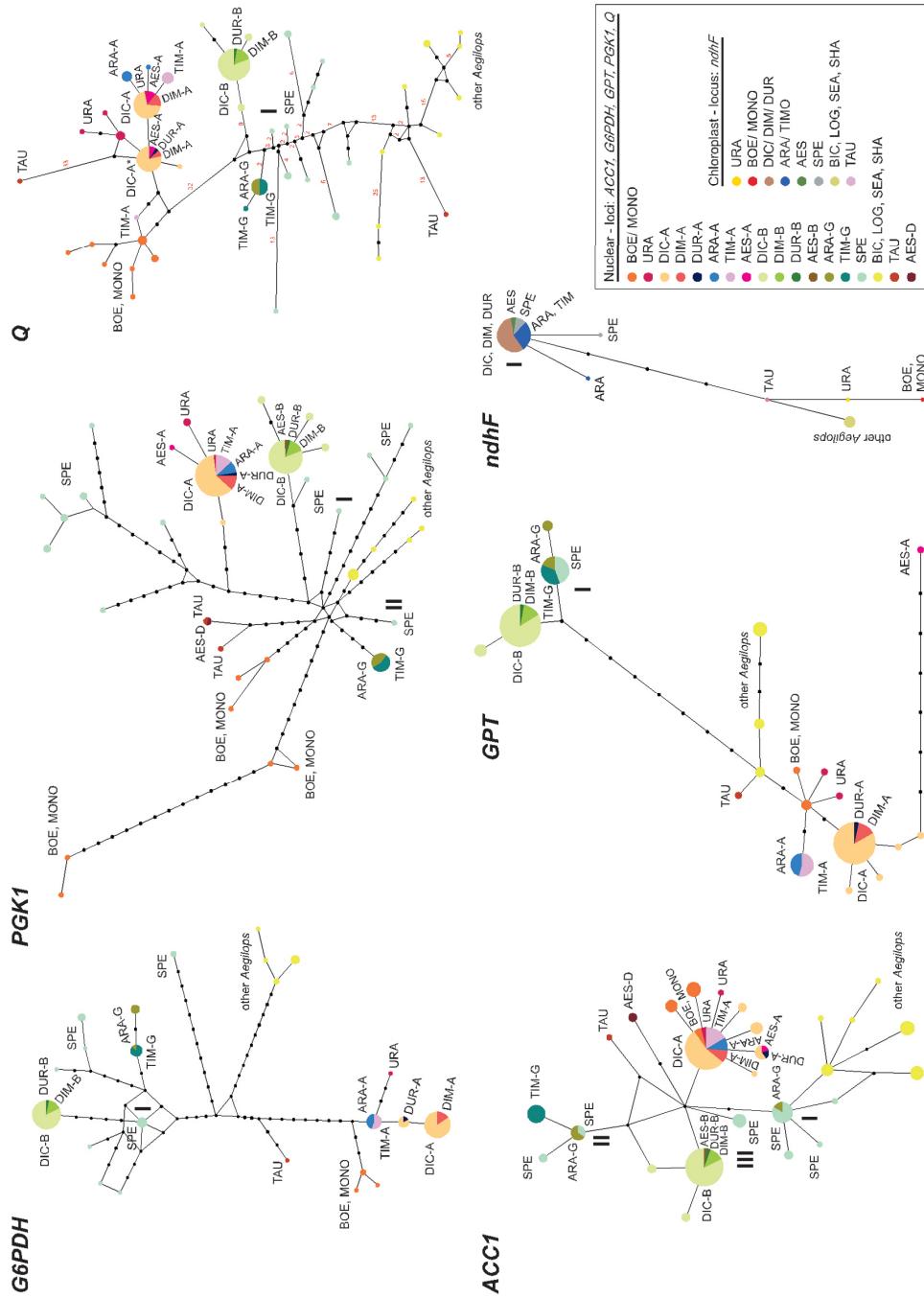


Fig. 4. - MJ networks derived from DNA sequence haplotypes among accessions, involving in all loci *Triticum dicoccoides* (34), *T. dicoccum* (5), *T. durum* (1), *Triticum urartu* (1), *Triticum timopheevii* (6), *Aegilops bicornis* (2), *Aegilops longissima* (2), *Aegilops searsii* (2), *Aegilops speltoides* (7), and *Aegilops tauschii* (1) plus additional haplotype data for each locus as available. Distance between 2 black dots is one nucleotide substitution. AES, *Triticum aestivum*; BOE, *Triticum boeticum*; DIC, *T. dicoccoides*; DIM, *T. dicoccum*; DUR, *T. durum*; LOG, *Ae. longissima*; MONO, *Triticum monococcum*; SEA, *Ae. searsii*; SHA, *Ae. sharonensis*; SPE, *Ae. speltoides*; TAU, *Ae. tauschii*; TIM, *T. timopheevii*; and URA, *Triticum urartu*. Species names according to Dorofeev et al. (1979) and Van Slageren (1994). *G6PDH*—For this MJ network, we used 72 lines from this project, for a total of 132 sequences *ACC1*—116 lines: 79 from this project; 37 from published results of other lines; total of 176 sequences: 139 from this project; 37 from published sequences. *GPT*—72: 71; 1, 124: 123, 1. *PGK1*—86: 76; 10, 144: 134; 10, *Q*: 93: 81, 12, 157: 145; 12, *ndhF*—79: 78; 1, 79: 78; 1.

Table 2. Heterozygosity among *Aegilops* accessions at loci sampled

Species	ACC1			G6PDH			GPT			PGK1			Q			VRNI		
	n ^a	H ^b	h ^c	n	H	h	n	H	h	n	H	h	n	H	h	n	H	h
<i>Ae. speltoides</i>	8	7	5	8	7	8	7	0	1	8	6	11	8	5	10	7	4	6
<i>Ae. bicornis</i>	2	0	1	2	0	2	2	0	1	2	0	2	2	0	2	2	0	1
<i>Ae. longissima</i>	2	1	3	2	0	1	2	0	1	2	0	1	2	1	3	2	0	1
<i>Ae. searsii</i>	2	0	1	2	0	1	2	0	1	2	0	2	2	0	2	2	0	1
<i>Ae. sharonensis</i>	2	0	1	2	0	1	2	0	1	2	0	1	2	1	2	2	0	1
<i>Ae. tauschii</i>	1	0	1	1	0	1	1	0	1	1	0	1	1	1	2	1	0	1

^a number of individuals sampled^b number of heterozygous individuals found^c number of haplotypes found (including publically available sequences)

1972; Fernandez-Calvin and Orellana 1994) in the absence of studies sampling many loci and accessions.

Our data indicate an origin of the B genome from within *Ae. speltoides*. First, the analysis of 375 AFLP loci links specifically polyploid wheats with *Ae. speltoides* to the exclusion of other Sitopsis species (fig. 3A). In addition, 65 AFLPs specific to the *T. aestivum* B genome link *Ae. speltoides* even more closely to the B and G genomes (fig. 3B). Second, with the exception of VRNI, haplotypes from chloroplast and nuclear loci show that *Ae. speltoides* shares the highest average sequence identity with the B and G genomes (table 3) and reveals specific progenitor-descendant relationships in the MJ networks (fig. 4). These findings can be incorporated into a broader scheme of wheat genome evolution (Supplementary fig. S2, Supplementary Material online) with resolved positions of the B genome relative to S progenitors and G sisters.

AABB and AAGG genome origins have been attributed to the same single hybridization event (Wagenaar 1961; Tanaka et al. 1979; Gill and Chen 1987; Provan et al. 2004) or to separate alloploidization events (Mori et al. 1995; Brown-Guedira et al. 1996; Rodriguez, Perera et al. 2000; Huang et al. 2002). In support of the former view, *T. dicoccoides* and *T. araraticum* have almost identical morphology, but they have F1 hybrids showing 100% sterility (Tanaka et al. 1979) with normal chromosome pairing (Rao and Smith 1968; Rawal and Harlan 1975; Tanaka et al. 1979). In addition, some lines of *T. araraticum* produce hybrids with a significant level of fertility when crossed to *T. dicoccoides* (Rao and Smith 1968; Rawal and Harlan 1975). Our data resolve this issue. The hybridization events leading to AABB and AAGG genomes occurred independently as evidenced 1) by their distinct positions in AFLP analyses, 2) by the finding that each has sequestered different samples of *Ae. speltoides* haplotype diversity, and 3) from the comparison of divergence within and among A, B, and G genome haplotypes (table 3). The B and G genomes are clearly distinct, incompatible with the view of a single-hybrid origin (Rodriguez, Maestra et al. 2002).

Wheat is no exception to the rule that specific polyploids arose recurrently during flowering plant evolution (Soltis 2005), accompanied by extensive and rapid genome restructuring (Leicht and Bennett 1997). Alloploidization often involves intergenomic recombination (McGrath et al. 1990; Jang and Gill 1994; Song et al. 1995; Soltis 2005) and rapid loss of DNA (Özkan et al. 2001), whereby subsequent diploidization restores disomic genetics (Levy and Feldman 2002). The genetic control of chromosome pairing provides insights on wheat alloplaid evolution. *Aegilops speltoides* forms are known that suppress pairing among homologous chromosomes (*Ph1* activity) (Aghaei-Sarbarzeh et al. 2000). If *Ph1* genotypes participate in polyploidization events, interspecific hybrids acquire a bivalent type of chromosome pairing, the case of *T. dicoccoides* (Sears 1976). Other lines of *A. speltoides* do not show *Ph1*-like activity (Kimber and Feldman 1987), having loci that suppress *Ph1*, thus allowing homologous pairing in interspecific crosses (Sears

Table 3. Average between- and within-genome haplotype sequence divergence (boldface: significant divergence between B to A and B to G comparisons)

Gene (L) ^d	$D_a \pm SE \times 10^3$ (n) ^a ; <i>T. dicoccoides</i> B vs.		Average sequence divergence within genomes			
	A genomes ^b	G genomes ^c	<i>T. dicoccoides</i> B	Other B ^e	<i>T. araraticum</i> G	<i>T. timopheevii</i> G
<i>ACC1</i> (366)	5.8 ± 0.4 (72)	7.7 ± 1.1 (15)	1.7 ± 1.9 (37)	1.5 ± 1.8 (43)	5.9 ± 5.7 (6)	4.2 ± 5.3 (15)
<i>G6PDH</i> (537)	49.7 ± 1.7 (56)	19.3 ± 1.6 (11)	0.0 ± 0.0 (34)	0.0 ± 0.0 (41)	1.7 ± 2.1 (5)	2.1 ± 2.1 (11)
<i>GPT</i> (673)	20.2 ± 0.8 (57)	3.6 ± 0.4 (11)	0.2 ± 0.6 (34)	0.2 ± 0.5 (40)	1.5 ± 1.0 (5)	1.2 ± 1.2 (11)
<i>PGK1</i> (665)	23.1 ± 1.4 (63)	20.6 ± 1.5 (11)	0.8 ± 1.3 (35)	0.7 ± 1.2 (41)	0.0 ± 0.0 (5)	0.0 ± 0.0 (11)
<i>Q</i> (917)	81.3 ± 2.3 (73)	21.7 ± 1.5 (11)	0.5 ± 0.8 (36)	0.4 ± 0.7 (43)	0.0 ± 0.0 (5)	0.2 ± 0.5 (11)
<i>VRN1</i> (304)	55.9 ± 1.8 (64)	6.8 ± 0.6 (11)	2.6 ± 2.2 (34)	2.5 ± 2.2 (41)	0.0 ± 0.0 (5)	0.0 ± 0.0 (11)

^a number of net nucleotide substitutions per site between populations ± SE (Nei 1987) calculated with DnaSP (Rozas et al. 2003) using the Jukes-Cantor method

^b n : number of loci sequenced for each species

^b A genomes of *T. monococcum*, *T. boeoticum*, *T. urartu*, *T. dicoccoides*, *T. durum*, *T. dicoccum*, *T. araraticum* and *T. timopheevii*

^c *T. araraticum* and *T. timopheevii*

^d number of sites compared, all gapped sites excluded.

^e *T. durum*, *T. dicoccum*

1976). The absence of *Ph1* or *Ph1*-like activity favors tetravalent formation and, possibly, intergenomic translocations. *Triticum araraticum* has extensive DNA loss (Özkan et al. 2001) and 6 chromosomal rearrangements relative to *T. dicoccoides* (Rodriguez et al. 2000a; Rodriguez et al. 2000b), 4 of which are intergenomic G–A translocations. A possibility is that in the AAGG genome synthesis, the *Ph1* allele of *Ae. speltoides* was suppressed and later restored via genetic segregation (today *T. araraticum* has an active *Ph1* allele). Similar evolutionary mechanisms may underlie the cytogenetic distinctness of S, B, and G genomes, whose evolutionary relationships are nonetheless revealed by AFLP and haplotype data.

Previous studies suggested that *T. araraticum* inherited a *Ae. speltoides* cytoplasm (Mori et al. 1997; Wang et al. 2000; Provan et al. 2004) but were conflicting for *T. dicoccoides* (Wang et al. 2000; Provan et al. 2004). Our *ndhF* data assign the *Ae. speltoides* cytoplasm to both *T. dicoccoides* and *T. araraticum*. This cytoplasm is distinct from that of other Sitopsis species.

We identified no *Ae. speltoides* line that shares greater similarity to all polyploids sampled than any other *Ae. speltoides* line. Furthermore, the *Ae. speltoides* haplotypes most similar or identical to B and G genome haplotypes are dispersed across different individual lines. Further sampling within *Ae. speltoides* might uncover lines that carry the same combination of haplotypes as the B genome donor contained. However, because the species is an outbreeder, it is more likely that no modern *Ae. speltoides* lines have preserved the B donor genotype in its contiguous ancestral state.

Supplementary Material

Supplementary material mentioned in the text, comprising 10 supplementary tables and 2 supplementary figures are available online at *Molecular Biology and Evolution* online (<http://www.mbe.oxfordjournals.org>). Sequence data from this article are deposited in GenBank Data library under accession no. provided in Supplementary table S10.

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CHAPTER 4

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Supplementary Material

I. Supplementary Tables

Supplementary Table S1. List of the 480 *Aegilops* accessions analysed and used for fig. 2

Supplementary Table S2. List of all the 1372 individual plants analysed, their origin and gene bank of provenience

Supplementary Table S3. List of the 850 unique lines selected among the 1372 lines in the initial screen

Supplementary Table S4. List of the 94 lines analyzed in fig. 3

Supplementary Table S5. Genes sequenced: references, chromosomal locations and functions

Supplementary Table S6. Lines used for sequence analysis

Supplementary Table S7. Publicly available sequences included in this study

Supplementary Table S8. Primers used for gene amplification and sequencing

Supplementary Table S9. Overview of the loci, their amplification conditions, fragment length, origin and chromosomal position for haplotype analyses

Supplementary Table S10. Genbank accession numbers for all new sequences reported in this research

II. Supplementary Figures

Supplementary Figure S1 - MJ network for *VRN1* haplotypes (82 lines, 137 sequences)

Supplementary Figure S2 - Overview of wheat evolution and events. *Aegilops* and *Triticum* nomenclature based on van Slageren (1994) and Dorofeev et al. (1979)

Supplementary Table S1. List of the 480 *Aegilops* accessions analyzed and used for figure 2

short names	ID-No	species names based on seedstore informations	collection site	origin
SPE-1	AE 92/94	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-2	AE 100/85	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-3	AE 101/91	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-4	AE 102/76	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-5	AE 104/76	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
BIC-6	AE 105/85	<i>Ae. bicornis</i> var. <i>bicornis</i>	unknown	IPK
BIC-7	AE 106/85	<i>Ae. bicornis</i> var. <i>bicornis</i>	unknown	IPK
LOG-8	AE 121/82	<i>Ae. longissima</i> subsp. <i>longissima</i>	unknown	IPK
LOG-9	AE 122/84	<i>Ae. longissima</i> subsp. <i>longissima</i>	unknown	IPK
LOG-11	AE 124/86	<i>Ae. longissima</i> subsp. <i>longissima</i>	unknown	IPK
LOG-12	AE 125/89	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel	IPK
SHA-13	AE 132/91	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SHA-14	AE 133/91	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SHA-15	AE 134/78	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SHA-16	AE 135/86	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SPE-17	AE 136/76	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-18	AE 137/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-19	AE 138/76	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-20	AE 139/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-21	AE 140/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
LOG-22	AE 315/78	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	Israel, Cesarea, coastal plain	IPK
SHA-23	AE 316/84	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	Israel	IPK
SHA-25	AE 318/84	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	Israel, between Tel Mond and Even, Yekuda, sharon plain	IPK
LOG-26	AE 319/82	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	Israel, Tantura, northern coastal plain	IPK
LOG-27	AE 320/82	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	Israel, northern coastal plain	IPK
LOG-28	AE 321/91	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	Israel, Tantura, northern coastal plain	IPK
SPE-30	AE 324/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, 4 km east A Shgeylon, coastal plain	IPK
SPE-31	AE 325/81	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, 33km sw Malatya	IPK
SPE-32	AE 326/80	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, Ashgelon, southern coastal plain	IPK
SPE-33	AE 327/80	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Turkey, 3 km south Tunceli	IPK
SPE-34	AE 328/91	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Turkey, 25 km west Tekirday	IPK
SPE-35	AE 329/76	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, 5 km east Acre	IPK
SPE-36	AE 330/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
LOG-39	AE 335/78	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, south of Petakh Tiqva	IPK
LOG-40	AE 337/81	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Gilat, 17 km nw Beersheba	IPK
SPE-41	AE 338/95	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, 17 km nw Beersheba	IPK
LOG-42	AE 339/78	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Raanana, southern coastal plain	IPK
LOG-43	AE 340/84	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Natanya, sharon plain	IPK
LOG-44	AE 341/79	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Natanya-Beit Lidd road, coastal plain	IPK
LOG-45	AE 342/79	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Shelfain, sharon plain	IPK
SPE-46	AE 345/81	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, Wadi Muzzara	IPK
SPE-48	AE 347/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Turkey, Yumurtalik	IPK

short names	ID-No	species names based on seedstore informations	collection site	origin
SPE-49	AE 348/78	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Turkey, 15 km south Mara	IPK
SPE-50	AE 349/78	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Israel, Technion campus, Haifa	IPK
SPE-51	AE 352/91	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, Giv'ot N. Negev	IPK
SPE-52	AE 377/76	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-53	AE 378/80	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-54	AE 379/00	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-55	AE 380/00	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-56	AE 383/78	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-57	AE 384/79	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-58	AE 385/78	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-59	AE 387/79	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-60	AE 368/80	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-61	AE 389/79	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-62	AE 397/82	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-63	AE 404/82	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Israel, 33 km sw Malatya	IPK
SPE-64	AE 405/82	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Israel, Ashkelon, southern coastal plain	IPK
SPE-65	AE 406/82	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Israel, 50 km south Ashdod, coastal plain	IPK
SPE-66	AE 407/82	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, Coilat, 17 km nw Beersheba	IPK
SPE-67	AE 408/82	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, 17 km nw Beersheba	IPK
LOG-71	AE 414/84	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, between Tel Mond and Even Yekuda, sharon plain	IPK
LOG-74	AE 417/78	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Tantura, northern coastal plain	IPK
SPE-76	AE 444/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SHA-77	AE 445/84	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SPE-78	AE 502/78	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-79	AE 505/94	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-80	AE 506/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-81	AE 513/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-82	AE 517/80	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Ukraine, Banat (Krim)	IPK
SPE-83	AE 522/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-84	AE 523/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-85	AE 533/94	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-86	AE 534/81	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-87	AE 535/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-88	AE 544/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-89	AE 544/91	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
LOG-90	AE 551/82	<i>Ae. longissima</i> subsp. <i>longissima</i>	unknown	IPK
SPE-91	AE 554/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-92	AE 564/78	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-93	AE 572/81	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SHA-94	AE 580/84	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SEA-95	AE 597/85	<i>Ae. searsii</i>	unknown	IPK
SPE-96	AE 624/89	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Syria, Suburbs of Ranthanah	IPK
SEA-97	AE 641/85	<i>Ae. searsii</i>	Syria, Suburbs of Gabagib	IPK
SEA-98	AE 642/89	<i>Ae. searsii</i>	Syria, Suburbs of Gabagib	IPK

SEA-99	AE 643/85	<i>Ae. searsii</i>	Syria, Suburbs of Gabajib
SEA-100	AE 679/90	<i>Ae. searsii</i>	Israel, Yaltin, near the pine forest
SPE-101	AE 684/83	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Portugal
SPE-002	AE 739/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Turkey, 38 km SE K. Maras
SPE-003	AE 747/83	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Turkey, 39 km E Kaitta
SPE-104	AE 748/84	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Turkey, Siverek
BIC-105	AE 788/85	<i>Ae. bicarinis</i> var. <i>mutica</i>	Lybia, Cyrenaika, 35 km W Mara Brega
SPE-106	AE 900/86	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Iraq, Eskikalak, Neinawa
LOG-108	AE 904/84	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel
LOG-109	AE 905/86	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel
SHA-110	AE 906/91	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	Israel
SPE-111	AE 915/86	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Portugal
SPE-112	AE 918/87	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Turkey
SPE-113	AE 921/87	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Iraq
SPE-114	AE 1026/91	<i>Ae. speltoides</i>	Israel
SPE-115	AE 1063/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria
SPE-116	AE 1064/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria
SPE-117	AE 1065/95	<i>Ae. speltoides</i>	Syria
SPE-118	AE 1066/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria
SEA-119	AE 1071/95	<i>Ae. searsii</i>	Jordan
SEA-120	AE 1072/97	<i>Ae. searsii</i>	Jordan
SEA-121	AE 1073/92	<i>Ae. searsii</i>	Jordan
SEA-122	AE 1074/93	<i>Ae. searsii</i>	Jordan
SEA-123	AE 1075/95	<i>Ae. searsii</i>	Jordan
SEA-124	AE 1076/92	<i>Ae. searsii</i>	Jordan
LOG-125	AE 1077/94	<i>Ae. longissima</i> subsp. <i>longissima</i>	Jordan
LOG-126	AE 1078/92	<i>Ae. longissima</i> subsp. <i>longissima</i>	Jordan
BIC-127	AE 1079/95	<i>Ae. bicarinis</i>	Jordan
BIC-128	AE 1080/95	<i>Ae. bicarinis</i>	Syria
SEA-129	AE 1081/97	<i>Ae. searsii</i>	Syria
SEA-130	AE 1083/97	<i>Ae. searsii</i>	Syria
SPE-131	AE 1084/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria
SPE-132	AE 1085/92	<i>Ae. speltoides</i>	Syria
SPE-133	AE 1086/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria
SHA-134	AE 1203/97	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel
BIC-135	Clae 47	<i>Ae. bicarinis</i>	unknown
BIC-136	Clae 70	<i>Ae. longissima</i>	unknown
LOG-137	PI 3304/86	<i>Ae. longissima</i>	Turkey, Izmir
LOG-138	PI 5421/96	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-139	PI 6041/03	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-140	PI 6041/04	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-142	PI 6041/06	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-143	PI 6041/07	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-144	PI 6041/08	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-145	PI 6041/09	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-146	PI 6041/10	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-147	PI 6041/11	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-148	PI 6041/12	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-149	PI 6041/14	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E

short names	ID-No	species names based on seedstore informations	collection site	origin
LOG-150	PI 604115	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E	USDA
LOG-151	PI 604118	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E	USDA
LOG-152	PI 604119	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E	USDA
LOG-153	PI 604120	<i>Ae. longissima</i>	Israel, Beit-Lid, 32°19' N, 34°54' E	USDA
LOG-154	PI 604121	<i>Ae. longissima</i>	Israel, Beit-Lid, 32°19' N, 34°54' E	USDA
LOG-155	PI 604122	<i>Ae. longissima</i>	Israel, Beit-Lid, 32°19' N, 34°54' E	USDA
LOG-156	PI 604123	<i>Ae. longissima</i>	Israel, Beit-Lid, 32°19' N, 34°54' E	USDA
LOG-157	PI 604124	<i>Ae. longissima</i>	Israel, Beit-Lid, 32°19' N, 34°54' E	USDA
LOG-159	PI 604126	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-160	PI 604129	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-161	PI 604130	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-162	PI 604131	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-163	PI 604132	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-164	PI 604133	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-165	PI 604134	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-166	PI 604135	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-167	PI 604136	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-168	PI 604137	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-169	PI 604138	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-170	PI 604139	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-171	PI 604140	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-172	PI 604141	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-173	PI 604142	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-174	PI 604143	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
LOG-175	PI 604144	<i>Ae. longissima</i>	Israel, Rehovot, 31°51' N, 34°48' E	USDA
SEA-176	PI 487284	<i>Ae. searsii</i>	Jordan, Kerak Province, 32°22' N, 35°42' E	USDA
SEA-177	PI 599121	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E	USDA
SEA-178	PI 599122	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E	USDA
SEA-179	PI 599123	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E	USDA
SEA-180	PI 599124	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E	USDA
SEA-181	PI 599125	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E	USDA
SEA-182	PI 599126	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E	USDA
SEA-183	PI 599128	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E	USDA
SEA-184	PI 599129	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E	USDA
SEA-185	PI 599130	<i>Ae. searsii</i>	Jordan, Tumeira, 32°23' N, 35°59' E	USDA
SEA-186	PI 599131	<i>Ae. searsii</i>	Jordan, El Bawieida, 32°21' N, 36°2' E	USDA
SEA-187	PI 599132	<i>Ae. searsii</i>	Jordan, Hailyan er Ruweibid, 32°15' N, 36°37' E	USDA
SEA-188	PI 599133	<i>Ae. searsii</i>	Jordan, El Madwar, 32°17' N, 35°59' E	USDA
SEA-189	PI 599134	<i>Ae. searsii</i>	Jordan, Balila, 32°22' N, 35°55' E	USDA
SEA-190	PI 599135	<i>Ae. searsii</i>	Jordan, Quaqfafa, 32°21' N, 35°56' E	USDA
SEA-191	PI 599136	<i>Ae. searsii</i>	Jordan, between El-Mastaba ad Jubba, 32°10' N, 35°52' E	USDA
SEA-192	PI 599137	<i>Ae. searsii</i>	Jordan, El Rawdha, 31°50' N, 35°47' E	USDA
SEA-193	PI 599138	<i>Ae. searsii</i>	Jordan, Jureina, 31°46' N, 35°43' E	USDA
SEA-194	PI 599139	<i>Ae. searsii</i>	Jordan, Ibb, 31°35' N, 35°41' E	USDA

SEA-195 PI 599140	<i>Ae. searsii</i>	Jordan, Rashadiya, 30° 41' N, 35° 45' E
SEA-196 PI 599142	<i>Ae. searsii</i>	Jordan, Mauta, 31° 4' N, 35° 41' E
SEA-197 PI 599143	<i>Ae. searsii</i>	Jordan, El-Hai, 30° 21' N, 35° 30' E
SEA-198 PI 599144	<i>Ae. searsii</i>	Jordan, Basta, 30° 14' N, 35° 31' E
SEA-199 PI 599145	<i>Ae. searsii</i>	Jordan, Er Rumeimin, 32° 7' N, 35° 48' E
SEA-200 PI 599146	<i>Ae. searsii</i>	Jordan, Jarash, 32° 15' N, 35° 55' E
SEA-201 PI 599147	<i>Ae. searsii</i>	Syria, El Hasim, 33° 5' N, 36° 33' E
SEA-202 PI 599148	<i>Ae. searsii</i>	Syria, Naddaya, 33° 41' N, 36° 7' E
SEA-203 PI 599149	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-204 PI 599150	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-205 PI 599151	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-206 PI 599152	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-207 PI 599153	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-208 PI 599154	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-209 PI 599155	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-210 PI 599156	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-211 PI 599157	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-212 PI 599158	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-213 PI 599159	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-214 PI 599160	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-215 PI 599161	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-216 PI 599162	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-217 PI 599163	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-218 PI 599164	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-219 PI 599165	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-220 PI 599166	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-221 PI 599167	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-222 PI 599168	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-223 PI 599169	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-224 PI 599170	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-225 PI 599171	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-226 PI 599172	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-227 PI 599173	<i>Ae. searsii</i>	Israel, Yattir Forest, 31° 21' N, 35° 7' E
SEA-228 PI 599174	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31° 58' N, 35° 20' E
SEA-229 PI 599175	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31° 58' N, 35° 20' E
SEA-230 PI 599177	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31° 58' N, 35° 20' E
LOG-231 Clae 32	<i>Ae. sharonensis</i>	Unknown
SHA-231 PI 542237	<i>Ae. sharonensis</i>	Turkey, Izmir
SHA-232 PI 584345	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E
SHA-233 PI 584346	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E
SHA-234 PI 584347	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E
SHA-235 PI 584348	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E
SHA-236 PI 584349	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E
SHA-237 PI 584350	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E
SHA-238 PI 584357	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E
SHA-239 PI 584358	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E
SHA-240 PI 584359	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E
SHA-241 PI 584360	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E
SHA-242 PI 584361	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E

short names	ID-No	species names based on seedstore informations	collection site	origin
SHA-244	PI 584362	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E	USDA
SHA-245	PI 584363	<i>Ae. sharonensis</i>	Israel, En-ha Mifraz, 32° 54' N, 35° 5' E	USDA
SHA-246	PI 584364	<i>Ae. sharonensis</i>	Israel, En-ha Mifraz, 32° 54' N, 35° 5' E	USDA
SHA-247	PI 584365	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E	USDA
SHA-248	PI 584366	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E	USDA
SHA-249	PI 584367	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E	USDA
SHA-250	PI 584368	<i>Ae. sharonensis</i>	Israel, Ben-Zakay I, 31° 51' N, 34° 43' E	USDA
SHA-251	PI 584369	<i>Ae. sharonensis</i>	Israel, Hefzi-Bah, 32° 28' N, 34° 53' E	USDA
SHA-252	PI 584370	<i>Ae. sharonensis</i>	Israel, Hefzi-Bah, 32° 28' N, 34° 53' E	USDA
SHA-253	PI 584371	<i>Ae. sharonensis</i>	Israel, Hefzi-Bah, 32° 28' N, 34° 53' E	USDA
SHA-254	PI 584372	<i>Ae. sharonensis</i>	Israel, Hefzi-Bah, 32° 28' N, 34° 53' E	USDA
SHA-255	PI 584374	<i>Ae. sharonensis</i>	Israel, Hefzi-Bah, 32° 28' N, 34° 53' E	USDA
SHA-256	PI 584376	<i>Ae. sharonensis</i>	Israel, Hefzi-Bah, 32° 28' N, 34° 53' E	USDA
SHA-257	PI 584377	<i>Ae. sharonensis</i>	Israel, Hefzi-Bah, 32° 28' N, 34° 53' E	USDA
SHA-258	PI 584378	<i>Ae. sharonensis</i>	Israel, En-haMifraz, 32° 54' N, 35° 5' E	USDA
SHA-259	PI 584379	<i>Ae. sharonensis</i>	Israel, En-haMifraz, 32° 54' N, 35° 5' E	USDA
SHA-260	PI 584380	<i>Ae. sharonensis</i>	Israel, Patah-Tiqwa, 32° 4' N, 34° 52' E	USDA
SHA-261	PI 584381	<i>Ae. sharonensis</i>	Israel, Patah-Tiqwa, 32° 4' N, 34° 52' E	USDA
SHA-262	PI 584382	<i>Ae. sharonensis</i>	Israel, Patah-Tiqwa, 32° 4' N, 34° 52' E	USDA
SHA-295	PI 584419	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-296	PI 584420	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-297	PI 584421	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-298	PI 584422	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-299	PI 584423	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-300	PI 584424	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-301	PI 584425	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-302	PI 584426	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-303	PI 584427	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-304	PI 584428	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-305	PI 584429	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-306	PI 584430	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-307	PI 584431	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-308	PI 584432	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-309	PI 584433	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-310	PI 584434	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-311	PI 584435	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-312	PI 584436	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-313	PI 584437	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-314	PI 584438	<i>Ae. speltoides</i>	Unknown	USDA
BIC-315	Clae 64	<i>Ae. speltoides</i>	Turkey, Kirkclareli, 41° 20' N, 27° 29' E	USDA
SPE-316	PI 170203	<i>Ae. speltoides</i>	Turkey, Kirkclareli, 41° 20' N, 27° 29' E	USDA
SPE-317	PI 170204	<i>Ae. speltoides</i>	Turkey, Diyarbakir, 37° 55' N, 40° 14' E	USDA
SPE-318	PI 172685	<i>Ae. speltoides</i>	Turkey, Siirt, 38° 3' N, 41° 45' E	USDA
SPE-319	PI 173614	<i>Ae. speltoides</i>		

SPE-320	PI 174010	<i>Ae. speltoides</i>	USDA
SPE-321	PI 219867	<i>Ae. speltoides</i>	USDA
SPE-322	PI 254865	<i>Ae. speltoides</i>	USDA
SPE-323	PI 369582	<i>Ae. speltoides</i>	USDA
SPE-324	PI 369593	<i>Ae. speltoides</i>	USDA
SPE-325	PI 369600	<i>Ae. speltoides</i>	USDA
SPE-326	PI 369612	<i>Ae. speltoides</i>	USDA
SPE-327	PI 369622	<i>Ae. speltoides</i>	USDA
SHA-262	PI 584382	<i>Ae. sharonensis</i>	USDA
SHA-263	PI 584383	<i>Ae. sharonensis</i>	USDA
SHA-264	PI 584385	<i>Ae. sharonensis</i>	USDA
SHA-265	PI 584386	<i>Ae. sharonensis</i>	USDA
SHA-266	PI 584388	<i>Ae. sharonensis</i>	USDA
SHA-267	PI 584389	<i>Ae. sharonensis</i>	USDA
SHA-268	PI 584390	<i>Ae. sharonensis</i>	USDA
SHA-269	PI 584391	<i>Ae. sharonensis</i>	USDA
SHA-270	PI 584392	<i>Ae. sharonensis</i>	USDA
SHA-271	PI 584393	<i>Ae. sharonensis</i>	USDA
SHA-272	PI 584394	<i>Ae. sharonensis</i>	USDA
SHA-273	PI 584395	<i>Ae. sharonensis</i>	USDA
SHA-274	PI 584396	<i>Ae. sharonensis</i>	USDA
SHA-275	PI 584397	<i>Ae. sharonensis</i>	USDA
SHA-276	PI 584398	<i>Ae. sharonensis</i>	USDA
SHA-277	PI 584399	<i>Ae. sharonensis</i>	USDA
BIC-278	PI 584400	<i>Ae. sharonensis</i>	USDA
BIC-279	PI 584401	<i>Ae. sharonensis</i>	USDA
SHA-280	PI 584402	<i>Ae. sharonensis</i>	USDA
SHA-281	PI 584403	<i>Ae. sharonensis</i>	USDA
SHA-282	PI 584404	<i>Ae. sharonensis</i>	USDA
SHA-283	PI 584406	<i>Ae. sharonensis</i>	USDA
SHA-284	PI 584407	<i>Ae. sharonensis</i>	USDA
SHA-285	PI 584408	<i>Ae. sharonensis</i>	USDA
SHA-286	PI 584409	<i>Ae. sharonensis</i>	USDA
SHA-287	PI 584410	<i>Ae. sharonensis</i>	USDA
SHA-288	PI 584412	<i>Ae. sharonensis</i>	USDA
SHA-289	PI 584413	<i>Ae. sharonensis</i>	USDA
SHA-290	PI 584414	<i>Ae. sharonensis</i>	USDA
SHA-291	PI 584415	<i>Ae. sharonensis</i>	USDA
SHA-292	PI 584416	<i>Ae. sharonensis</i>	USDA
SHA-293	PI 584417	<i>Ae. sharonensis</i>	USDA
SHA-294	PI 584418	<i>Ae. sharonensis</i>	USDA
SPE-328	PI 449339	<i>Ae. speltoides</i>	USDA
SPE-329	PI 449340	<i>Ae. speltoides</i>	USDA
SPE-330	PI 486262	<i>Ae. speltoides</i>	USDA
SPE-331	PI 486263	<i>Ae. speltoides</i>	USDA
SPE-332	PI 486264	<i>Ae. speltoides</i>	USDA
SPE-333	PI 487231	<i>Ae. speltoides</i>	USDA
SPE-334	PI 487232	<i>Ae. speltoides</i>	USDA
SPE-335	PI 487233	<i>Ae. speltoides</i>	USDA

short names	ID-No	species names based on seedstore informations	collection site	origin
SPE-236	PI 487235	<i>Ae. speltoides</i>	Syria, Latakia, 35°40'N, 35°52'E	USDA
SPE-237	PI 487237	<i>Ae. speltoides</i>	Syria, Latakia, 35°53'N, 35°48'E	USDA
SPE-238	PI 487238	<i>Ae. speltoides</i>	Syria, Tartus, 35°7'N, 36°7'E	USDA
SPE-239	PI 499261	<i>Ae. speltoides</i>	China, 35°0'N, 105°0'E	USDA
SPE-240	PI 542238	<i>Ae. speltoides</i>	Turkey, Diyarbakir, 37°38'N, 40°20'E	USDA
SPE-241	PI 573448	<i>Ae. speltoides</i>	Turkey, Cankiri, 40°31'N, 33°38'E	USDA
SPE-242	PI 573449	<i>Ae. speltoides</i>	Turkey, Cankiri, 40°31'N, 33°38'E	USDA
SPE-243	PI 573450	<i>Ae. speltoides</i>	Turkey, Ankara, 40°2'N, 32°55'E	USDA
SPE-244	PI 573452	<i>Ae. speltoides</i>	Turkey, Ankara, 40°2'N, 32°55'E	USDA
SPE-245	PI 542245	<i>Ae. speltoides</i> var. <i>ligustica</i>	Turkey, Urfa, 36°56'N, 38°55'E	USDA
SPE-246	PI 542256	<i>Ae. speltoides</i> var. <i>ligustica</i>	Turkey, Adiyaman, 37°58'N, 38°37'E	USDA
SPE-247	PI 560527	<i>Ae. speltoides</i> var. <i>ligustica</i>	Turkey, Mus, 38°49'N, 41°35'E	USDA
SPE-248	PI 560528	<i>Ae. speltoides</i> var. <i>ligustica</i>	Turkey, Siirt, 37°45'N, 42°10'E	USDA
SPE-249	PI 542269	<i>Ae. speltoides</i> var. <i>speltoides</i>	Turkey, Gaziantep, 37°55'N, 37°24'E	USDA
SPE-250	PI 542273	<i>Ae. speltoides</i> var. <i>speltoides</i>	Turkey, Adiyaman, 37°40'N, 37°57'E	USDA
SPE-251	PI 542274	<i>Ae. speltoides</i> var. <i>speltoides</i>	Turkey, Adiyaman, 38°1'N, 38°31'E	USDA
SPE-252	PI 560530	<i>Ae. speltoides</i> var. <i>speltoides</i>	Turkey, Siirt, 38°4'N, 41°47'E	USDA
SPE-253	PI 560531	<i>Ae. speltoides</i> var. <i>speltoides</i>	Turkey, Siirt, 37°45'N, 42°10'E	USDA
SPE-254	PI 560748	<i>Ae. speltoides</i> var. <i>speltoides</i>	Turkey, Siirt, 37°56'N, 42°16'E	USDA
SPE-255	PI 560751	<i>Ae. speltoides</i> var. <i>speltoides</i>	Turkey, Siirt, 37°58'N, 42°21'E	USDA
SHA-357	TA 2065	<i>Ae. sharonensis</i>	Turkey, Elazig, 16 km NW of Elazig	WGRC
SEA-358	TA 2343	<i>Ae. searsii</i>	Syria, Damascus, Suburbs of Ghabaghish	WGRC
SEA-359	TA 2353	<i>Ae. searsii</i>	Jordan, West Bank, Yattir, 4-5 km NE of the park watchman's house, 10-15 km SE of Hebron	WGRC
LOG-360	TA 1912	<i>Ae. longissima</i>	Israel, 3 km SE of Rehovot	WGRC
LOG-361	TA 1921	<i>Ae. longissima</i> subsp. <i>nova</i>	Jordan, Al Balqa'; Basin of the Jordan River, 32°34'N, 36°0'E	WGRC
BIC-362	TA 1945	<i>Ae. bicornis</i> subsp. <i>typica</i>	Egypt, Marsa Matruh; 21 km W of Alexandria, 33°15'N, 29°40'E	WGRC
SEA-364	TE 01	<i>Ae. searsii</i>	Israel, Yattir, southern Judea	WIS
SEA-365	TE 07	<i>Ae. searsii</i>	Israel, Kufar Fajer, Judea	WIS
SEA-366	TE 08	<i>Ae. searsii</i>	South of Dabarja, Hebron-BEERSheva Road	WIS
SEA-367	TE 10	<i>Ae. searsii</i>	Israel, East of Taiyiba, Samaria	WIS
SEA-369	TE 16	<i>Ae. searsii</i>	Syria, Gabagib	WIS
SEA-370	TE 17	<i>Ae. searsii</i>	Syria, Ramtha	WIS
SEA-371	TE 19	<i>Ae. searsii</i>	Syria, Gabagib	WIS
SEA-372	TE 25	<i>Ae. searsii</i>	Israel, East of Lahav, Southwestern Judea	WIS
SEA-373	TE 36	<i>Ae. searsii</i>	Syria (From Karl Hammer, #AE633/85)	WIS
BIC-374	TB 01	<i>Ae. bicornis</i>	From Sears (P60-39-1)	WIS
BIC-375	TB 02	<i>Ae. bicornis</i>	Israel, East of Revivim-Gevulot-Magen intersectin, Western Negev	WIS
BIC-376	TB 05	<i>Ae. bicornis</i>	Egypt, Matruch	WIS
BIC-377	TB 07	<i>Ae. bicornis</i>	Egypt, West of Alexandria	WIS
BIC-378	TB 08	<i>Ae. bicornis</i>	Rafiah-El Arish Road, Northwestern Sinai	WIS
BIC-379	TB 10	<i>Ae. bicornis</i>	Israel, Ein-Yorkeam, Central Negev	WIS
BIC-380	TB 19	<i>Ae. bicornis</i>	Lybia (from Karl Hammer #AE788/92)	WIS
SHA-381	TH 01	<i>Ae. sharonensis</i>	Israel, Caesarea, Coastal Plain	WIS
SHA-382	TH 02	<i>Ae. sharonensis</i>	Israel, Naaman salt-marsh, near Acre	WIS

TH 04	WIS
SHA-383	Israel, Rehovot, Coastal Plain,
SHA-384	Israel, North of Haifa
LOG-385	Israel, Revivim, Central Negev
LOG-386	Israel, Rehovot, Coastal plain
LOG-388	Israel, Nahariyya-Rosh Hanikra Road, Western Galilee
LOG-389	Israel, Hadera-Karkur Road, Coastal plain
LOG-392	Israel, East of Ein Gev, East of the lake of Galilee
SPE-393	Israel, East of Ashkelon, Southern Coastal Plain
SPE-394	Israel, Ein Ayyala, South of Haifa
SPE-395	Israel, North Of Zichron-Yaakov
SPE-396	Israel, Wadi Hlazon, Western Galilee
SPE-397	Israel, East of Givat-Koah, Shefela
SPE-398	Israel, Akhikhud Junction, Western Galilee
LOG-399	Israel, Herzlia
LOG-400	Jordan, 16 km E of Dead Sea
LOG-401	Jordan, Basin of the Jordan river
LOG-402	Israel, Gesher haZiw, N of Nahariyya
LOG-403	Israel, Beit Hananya, N of Zikhron Ya'akov
LOG-404	Israel, Netanya, S of haSharon
LOG-405	Israel, Rishon leZiyon
LOG-406	Israel, Ziqim
LOG-407	Israel, ca. 12km NW of Ze'elim, NE of Ammi' oz
LOG-408	Israel, ca. 8 km S of Qiryat Gat, S of Ahuzzam
LOG-409	Israel, NE of Be'er Sheva
LOG-410	Israel, SE of Dimona
LOG-411	Israel, ca. 25 km S of Be'er Sheva, W of Mashabbim
LOG-412	Israel, 6 km N of Mizpe Ramon
SEA-413	Jordan, 13 km N of Hebron
SEA-414	Syria, Suburbs of Gabagib
SEA-415	Syria, Suburbs of Ramtha
SEA-416	Syria, Suburbs of Gabagib
SEA-417	Syria, Suburbs of Gabagib
SEA-418	Jordan, 27 km before Jarash coming from Ramtha, Irbid; 32°27'N, 35°55'E
SEA-419	Jordan, road from Mafraq to Jarash, 13 km after Mafraq, Irbid; 32°18'N, 36°10'E
SEA-420	Jordan, 6 km S of Madaba, Amman; 31°37'N, 35°48'E
SEA-421	Jordan, 6 km S of Madaba, Amman, 31°37'N, 35°48'E
SEA-422	Jordan, 20 km S of the junction Amman - Desert road; 31°37'N, 36°2'E
SEA-423	Israel, Gittit, 9 km W of Massa'a
SEA-424	Israel, W of Kokhav haShahar
SEA-425	Israel, Kokhav haShahar
SEA-426	Israel, ca. 32 km NW of Jericho
SEA-427	Israel, 3 km E of Ma'ale Mikhmas
SEA-428	Israel, Mahane Yattir, NE of Be'er Sheva
SEA-429	Israel, N of Har amassa Nature Reserve, E of Mahane Yattir
SEA-430	Israel, NW of Arad, 8 km N of Tel Arad
SHA-431	Israel, near Cesarea, Sharon plain
SHA-432	Israel, near Maagan Michael
SHA-433	Israel, Ein Hamifratz, S of Akko
SHA-434	Israel, Haifa, Qishon

short names	ID-No	species names based on seedstore informations	collection site	origin
SHA-435	14663	<i>Ae. sharonensis</i>	Israel, haBonim	Kyoto
SHA-436	14664	<i>Ae. sharonensis</i>	Israel, Caesarea	Kyoto
SHA-437	14665	<i>Ae. sharonensis</i>	Israel, Caesarea	Kyoto
SHA-438	14666	<i>Ae. sharonensis</i>	Israel, NE of Giv'at Olga	Kyoto
SHA-439	14667	<i>Ae. sharonensis</i>	Israel, Mikhmoret, 10 km S of Hadera	Kyoto
SHA-440	14668	<i>Ae. sharonensis</i>	Israel, Wingate, S of Netanya	Kyoto
SHA-441	14669	<i>Ae. sharonensis</i>	Israel, Zahara, N of Tel Aviv	Kyoto
SHA-442	14670	<i>Ae. sharonensis</i>	Israel, near Soreq Nuclear Center	Kyoto
SHA-443	14671	<i>Ae. sharonensis</i>	Israel, N of Aashdod	Kyoto
SHA-444	14672	<i>Ae. sharonensis</i>	Israel, S of Ashqeron	Kyoto
SHA-445	14673	<i>Ae. sharonensis</i>	Israel, Ziqim	Kyoto
BIC-446	3 - 2	<i>Ae. bicornis</i>	Israel 60 km W of Beer-Sheba	Kyoto
BIC-447	3 - 3	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-448	5782	<i>Ae. bicornis</i>	Egypt, Matruh	Kyoto
BIC-449	5783	<i>Ae. bicornis</i>	Egypt, Matruh	Kyoto
BIC-451	5786	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-452	5787	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-453	5788	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-454	5790	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-455	5793	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-456	6141 A	<i>Ae. bicornis</i>	Jordan, 85 km NE of Aqaba; 29°55'E, 35°23'N	Kyoto
BIC-457	6141 B	<i>Ae. bicornis</i>	Jordan, 85 km NE of Aqaba; 29°55'E, 35°23'N	Kyoto
BIC-458	14610	<i>Ae. bicornis</i>	Israel, near Soreq Nuclear Center	Kyoto
BIC-459	14612	<i>Ae. bicornis</i>	Israel, Nir Yizhaq	Kyoto
BIC-460	14614 A	<i>Ae. bicornis</i>	Israel, roadside along Hwy 222 from Gevulot Junction to Gevulot	Kyoto
BIC-461	14615	<i>Ae. bicornis</i>	Israel, Gevulot	Kyoto
BIC-462	15002	<i>Ae. bicornis</i>	Egypt, 40 km E from El Arish	Kyoto
BIC-463	15004	<i>Ae. bicornis</i>	Egypt, Gamasa	Kyoto
BIC-464	15006	<i>Ae. bicornis</i>	Egypt, Balutin	Kyoto
BIC-465	15008	<i>Ae. bicornis</i>	Egypt, Balutin, eastside of the town	Kyoto
BIC-466	15010	<i>Ae. bicornis</i>	Egypt, W of Rashid	Kyoto
BIC-467	15012	<i>Ae. bicornis</i>	Egypt, E of Alexandria	Kyoto
LOG-468	TL 12	<i>Ae. longissima</i>	South of Yad-Mordekhai, Southern Coastal Plain, Israel	WIS
TAU-469	TUR 02554	<i>Ae. tauschii</i>	Sanliurfa/Turkey	FCCRI
TAU-470	TUR 02564	<i>Ae. tauschii</i>	Sanliurfa/Turkey	FCCRI
SPE-471	TUR 03502	<i>Ae. speltoides</i>	Mersin/Mersin	FCCRI
SPE-472	TUR 01498	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-473	TUR 02776	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-474	TUR 02785	<i>Ae. speltoides</i>	Gaziantep/Turkey	FCCRI
SPE-475	TUR 00623	<i>Ae. speltoides</i>	Adiyaman/Turkey	FCCRI
SPE-476	TUR 03355	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-477	TUR 03354	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-478	TUR 00903	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-479	TUR 02556	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI

SPE-480	TUR 02774	<i>Ae. speltooides</i>	FCCRI
SPE-481	TUR 01751	<i>Ae. speltooides</i>	FCCRI
SPE-482	TUR 00301	<i>Ae. speltooides</i>	FCCRI
SPE-483	TUR 03498	<i>Ae. speltooides</i>	FCCRI
SPE-484	TUR 02764	<i>Ae. speltooides</i>	FCCRI
SPE-485	TUR 01725	<i>Ae. speltooides</i>	FCCRI
SPE-486	TUR 03425	<i>Ae. speltooides</i>	FCCRI
SPE-487	TUR 02592	<i>Ae. speltooides</i>	FCCRI
SPE-488	TUR 03374	<i>Ae. speltooides</i>	FCCRI
SPE-489	TUR 03352	<i>Ae. speltooides</i>	FCCRI
SPE-490	TUR 01191	<i>Ae. speltooides</i>	FCCRI
SPE-491	TUR 00488	<i>Ae. speltooides</i>	FCCRI
SPE-492	TUR 03384	<i>Ae. speltooides</i>	FCCRI
SPE-493	TUR 00634	<i>Ae. speltooides</i>	FCCRI
SPE-494	TUR 03416	<i>Ae. speltooides</i>	FCCRI
SPE-495	TUR 01765	<i>Ae. speltooides</i>	FCCRI
SPE-496	TUR 01642	<i>Ae. speltooides</i>	FCCRI
SPE-497	TUR 01690	<i>Ae. speltooides</i>	FCCRI
SPE-498	TUR 03287	<i>Ae. speltooides</i>	FCCRI
SPE-499	TUR 02210	<i>Ae. speltooides</i>	FCCRI
SPE-500	TUR 01689	<i>Ae. speltooides</i>	FCCRI
SPE-501	TUR 01636	<i>Ae. speltooides</i>	FCCRI

Supplementary Table S2. List of all the 1372 individual plants analyzed their origin and gene bank of provenience

<i>Aegilops</i> -No	Accession-No	Species	Origin	Source
SPE-1/2	AE 92/94	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-1/3	AE 92/94	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-1/4	AE 92/94	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-2/1	AE 100/85	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-2/2	AE 100/85	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-2/3	AE 100/85	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-3/1	AE 101/91	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-3/2	AE 101/91	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-3/3	AE 101/91	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-4/3	AE 102/76	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-4/4	AE 102/76	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-5/1	AE 104/76	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-5/2	AE 104/76	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-5/3	AE 104/76	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
BIC-6/1	AE 105/85	<i>Ae. bicornis</i> var. <i>bicornis</i>	unknown	IPK
BIC-6/2	AE 105/85	<i>Ae. bicornis</i> var. <i>bicornis</i>	unknown	IPK
BIC-6/3	AE 105/85	<i>Ae. bicornis</i> var. <i>bicornis</i>	unknown	IPK
BIC-6/4	AE 105/85	<i>Ae. bicornis</i> var. <i>bicornis</i>	unknown	IPK
BIC-7/2	AE 106/85	<i>Ae. bicornis</i> var. <i>bicornis</i>	unknown	IPK
BIC-7/3	AE 106/85	<i>Ae. bicornis</i> var. <i>bicornis</i>	unknown	IPK
BIC-7/4	AE 106/85	<i>Ae. bicornis</i> var. <i>bicornis</i>	unknown	IPK
LOG-8/3	AE 121/82	<i>Ae. longissima</i> subsp. <i>longissima</i>	unknown	IPK
LOG-9/1	AE 122/84	<i>Ae. longissima</i> subsp. <i>longissima</i>	unknown	IPK
LOG-9/3	AE 122/84	<i>Ae. longissima</i> subsp. <i>longissima</i>	unknown	IPK
LOG-9/4	AE 122/84	<i>Ae. longissima</i> subsp. <i>longissima</i>	unknown	IPK
LOG-11/1	AE 124/86	<i>Ae. longissima</i> subsp. <i>longissima</i>	unknown	IPK
LOG-11/2	AE 124/86	<i>Ae. longissima</i> subsp. <i>longissima</i>	unknown	IPK
LOG-12/4	AE 125/89	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel	IPK
SHA-13/1	AE 132/91	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SHA-13/3	AE 132/91	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SHA-14/1	AE 133/91	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SHA-14/2	AE 133/91	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SHA-14/3	AE 133/91	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SHA-15/2	AE 134/78	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SHA-15/3	AE 134/78	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SHA-16/1	AE 135/86	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SHA-16/2	AE 135/86	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SHA-16/3	AE 135/86	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SPE-17/2	AE 136/76	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-17/3	AE 136/76	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-17/4	AE 136/76	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-18/2	AE 137/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-18/3	AE 137/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-19/1	AE 138/76	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK

AE 138/76	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
AE 138/76	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
AE 139/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
AE 139/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
AE 139/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
AE 139/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
AE 140/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
AE 140/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
AE 140/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
AE 315/78	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	IPK
AE 315/78	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	IPK
SHA-23/5	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	IPK
SHA-25/2	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	IPK
SHA-25/3	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	IPK
LOG-26/1	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	IPK
LOG-26/2	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	IPK
LOG-26/2	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	IPK
LOG-26/3	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	IPK
LOG-27/1	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-27/2	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-27/3	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-28/1	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-28/2	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-28/3	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
SPE-20/1	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-20/2	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-20/3	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-31/1	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-31/2	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-31/3	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-32/2	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-32/5	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-33/2	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-33/4	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-34/1	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-34/2	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-34/3	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-35/1	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-35/2	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-36/1	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-36/2	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-36/3	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
LOG-39/1	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-39/2	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-39/3	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-40/2	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-40/5	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
SPE-41/1	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-41/2	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-41/3	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
LOG-42/1	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK

<i>Aegilops</i> -No	Accession-No	Species	Origin	Source
LOG-42/2	AE 339/78	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Raanana, southern coastal plain	IPK
LOG-42/4	AE 339/78	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Raanana, southern coastal plain	IPK
LOG-43/1	AE 340/84	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Natanya, sharon plain	IPK
LOG-43/3	AE 340/84	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Natanya, sharon plain	IPK
LOG-43/4	AE 340/84	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Natanya, sharon plain	IPK
LOG-44/1	AE 341/79	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Natanya-Beit Lidd road, coastal plain	IPK
LOG-44/2	AE 341/79	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Natanya-Beit Lidd road, coastal plain	IPK
LOG-44/3	AE 341/79	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Natanya-Beit Lidd road, coastal plain	IPK
LOG-45/1	AE 342/79	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Shelfain, sharon plain	IPK
LOG-45/2	AE 342/79	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Shelfain, sharon plain	IPK
LOG-45/3	AE 342/79	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel, Shelfain, sharon plain	IPK
SPE-46/2	AE 345/81	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, Wadi Muzzara	IPK
SPE-46/3	AE 345/81	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, Wadi Muzzara	IPK
SPE-48/1	AE 347/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Turkey, Yumurtalik	IPK
SPE-48/2	AE 347/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Turkey, Yumurtalik	IPK
SPE-48/4	AE 347/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Turkey, Yumurtalik	IPK
SPE-49/1	AE 348/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Turkey, 15 km south Mara	IPK
SPE-49/3	AE 348/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Turkey, 15 km south Mara	IPK
SPE-49/4	AE 348/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Turkey, 15 km south Mara	IPK
SPE-50/1	AE 349/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Israel, Technion campus, Haifa	IPK
SPE-50/3	AE 349/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Israel, Technion campus, Haifa	IPK
SPE-50/4	AE 349/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Israel, Technion campus, Haifa	IPK
SPE-51/1	AE 352/91	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, Goulot, N. Negev	IPK
SPE-51/2	AE 352/91	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, Goulot, N. Negev	IPK
SPE-51/3	AE 352/91	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Israel, Goulot, N. Negev	IPK
SPE-52/1	AE 377/76	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-52/2	AE 377/76	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-52/3	AE 377/76	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-53/2	AE 378/80	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-53/3	AE 378/80	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-53/5	AE 378/80	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-54/1	AE 379/00	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-54/2	AE 379/00	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-54/3	AE 379/00	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-55/2	AE 380/00	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-55/4	AE 380/00	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-55/5	AE 380/00	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-56/1	AE 383/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-56/2	AE 383/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-56/4	AE 383/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-57/1	AE 384/79	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-57/2	AE 384/79	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-57/3	AE 384/79	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK
SPE-58/1	AE 385/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	unknown	IPK

SPE-58/3	AE 385/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-58/4	AE 385/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-59/1	AE 387/79	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-59/2	AE 387/79	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-59/3	AE 387/79	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-60/2	AE 388/80	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-60/3	AE 388/80	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-61/1	AE 389/79	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-61/2	AE 389/79	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-61/3	AE 389/79	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-62/1	AE 397/82	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-62/5	AE 397/82	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-63/2	AE 404/82	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-63/3	AE 404/82	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-64/1	AE 405/82	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-64/2	AE 405/82	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-64/4	AE 405/82	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-65/1	AE 406/82	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-65/5	AE 406/82	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-66/1	AE 407/82	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-66/2	AE 407/82	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-66/3	AE 407/82	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-67/2	AE 408/82	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-67/3	AE 408/82	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-67/4	AE 408/82	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
LOG-71/1	AE 414/84	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-71/2	AE 414/84	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-71/3	AE 414/84	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-74/1	AE 417/78	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-74/2	AE 417/78	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
LOG-74/4	AE 417/78	<i>Ae. longissima</i> subsp. <i>longissima</i>	IPK
SPE-76/1	AE 444/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-76/3	AE 444/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-76/4	AE 444/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SHA-77/1	AE 445/84	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	IPK
SHA-77/3	AE 445/84	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	IPK
SHA-77/5	AE 445/84	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	IPK
SPE-78/1	AE 502/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-78/2	AE 502/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-78/3	AE 502/78	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	IPK
SPE-79/1	AE 505/94	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-79/2	AE 505/94	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-79/3	AE 505/94	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-80/1	AE 506/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-80/2	AE 506/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-80/3	AE 506/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-81/1	AE 513/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-81/2	AE 513/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK
SPE-81/3	AE 513/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	IPK

<i>Aegilops</i> -No	Accession-No	Species	Origin	Source
SPE-82/1	AE 517/80	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Ukraine, Banat (Krim)	IPK
SPE-82/2	AE 517/80	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Ukraine, Banat (Krim)	IPK
SPE-82/3	AE 517/80	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Ukraine, Banat (Krim)	IPK
SPE-83/2	AE 522/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-83/3	AE 522/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-83/4	AE 522/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-84/1	AE 523/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-84/2	AE 523/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-84/3	AE 523/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-85/1	AE 533/94	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-85/2	AE 533/94	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-85/3	AE 533/94	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-86/1	AE 534/81	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-86/2	AE 534/81	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-86/3	AE 534/81	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-87/1	AE 535/78	<i>Ae. speltoides</i>	unknown	IPK
SPE-87/2	AE 535/78	<i>Ae. speltoides</i>	unknown	IPK
SPE-87/3	AE 535/78	<i>Ae. speltoides</i>	unknown	IPK
SPE-88/2	AE 544/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-88/3	AE 544/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-88/4	AE 544/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-89/1	AE 544/91	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-89/2	AE 544/91	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-89/3	AE 544/91	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
LOG-90/1	AE 551/82	<i>Ae. longissima</i> subsp. <i>longissima</i>	unknown	IPK
LOG-90/2	AE 551/82	<i>Ae. longissima</i> subsp. <i>longissima</i>	unknown	IPK
SPE-91/1	AE 554/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-91/2	AE 554/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-91/3	AE 554/78	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-92/1	AE 564/78	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-92/2	AE 564/78	<i>Ae. longissima</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-92/4	AE 564/78	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-92/5	AE 564/78	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	unknown	IPK
SPE-93/1	AE 572/81	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-93/2	AE 572/81	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-93/3	AE 572/81	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SHA-94/1	AE 580/84	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SEA-94/2	AE 580/84	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	unknown	IPK
SEA-95/1	AE 597/85	<i>Ae. searsii</i>	unknown	IPK
SEA-95/2	AE 597/85	<i>Ae. searsii</i>	unknown	IPK
SEA-95/3	AE 597/85	<i>Ae. searsii</i>	unknown	IPK
SPE-96/1	AE 624/89	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-96/2	AE 624/89	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK
SPE-96/3	AE 624/89	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	unknown	IPK

SEA-971	<i>Ae. searsii</i>	Syria, Suburbs of Ranttha	IPK
SEA-972	<i>Ae. searsii</i>	Syria, Suburbs of Ranttha	IPK
SEA-973	<i>Ae. searsii</i>	Syria, Suburbs of Ranttha	IPK
SEA-981	<i>Ae. searsii</i>	Syria, Suburbs of Gabagib	IPK
SEA-982	<i>Ae. searsii</i>	Syria, Suburbs of Gabagib	IPK
SEA-983	<i>Ae. searsii</i>	Syria, Suburbs of Gabagib	IPK
SEA-99/1	<i>Ae. searsii</i>	Syria, Suburbs of Gabajib	IPK
SEA-99/2	<i>Ae. searsii</i>	Syria, Suburbs of Gabajib	IPK
SEA-99/3	<i>Ae. searsii</i>	Syria, Suburbs of Gabajib	IPK
SEA-100/1	<i>Ae. searsii</i>	Israel, Yaltin, near the pine forest	IPK
SEA-100/2	<i>Ae. searsii</i>	Israel, Yaltin, near the pine forest	IPK
SEA-100/3	<i>Ae. searsii</i>	Israel, Yaltin, near the pine forest	IPK
SPE-101/1	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Portugal	IPK
SPE-101/2	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Portugal	IPK
SPE-101/3	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Turkey, 38 km SE K. Maras	IPK
SPE-102/1	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Turkey, 38 km SE K. Maras	IPK
SPE-102/3	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Turkey, 39 km E Kahita	IPK
SPE-103/1	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Turkey, 39 km E Kahita	IPK
SPE-103/2	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Turkey, 39 km E Kahita	IPK
SPE-103/3	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Turkey, 39 km E Kahita	IPK
SPE-104/1	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Turkey, Siverek	IPK
SPE-104/2	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Turkey, Siverek	IPK
SPE-104/4	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Turkey, Siverek	IPK
BIC-105/1	<i>Ae. bicornis</i> var. <i>mutica</i>	Lybia, Cyrenaika, 35 km W Mara Brega	IPK
BIC-105/2	<i>Ae. bicornis</i> var. <i>mutica</i>	Lybia, Cyrenaika, 35 km W Mara Brega	IPK
BIC-105/3	<i>Ae. bicornis</i> var. <i>mutica</i>	Lybia, Cyrenaika, 35 km W Mara Brega	IPK
SPE-106/1	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Iraq, Eskikalak, Neinawa	IPK
SPE-106/2	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Iraq, Eskikalak, Neinawa	IPK
SPE-106/3	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Israel	IPK
LOG-108/1	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel	IPK
LOG-108/3	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel	IPK
LOG-108/4	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel	IPK
LOG-109/1	<i>Ae. longissima</i> subsp. <i>sharonensis</i>	Israel	IPK
LOG-109/2	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Portugal	IPK
LOG-109/3	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Portugal	IPK
SHA-110/1	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Turkey	IPK
SHA-110/2	<i>Ae. speltoides</i> subsp. <i>ligustica</i>	Turkey	IPK
SPE-111/1	<i>Ae. 915/86</i>	Iraq	IPK
SPE-111/2	<i>Ae. 915/86</i>	Israel	IPK
SPE-111/3	<i>Ae. 915/86</i>	Israel	IPK
SPE-112/1	<i>Ae. 918/87</i>	Israel	IPK
SPE-112/2	<i>Ae. 918/87</i>	Portugal	IPK
SPE-112/3	<i>Ae. 918/87</i>	Portugal	IPK
SPE-113/1	<i>Ae. 921/87</i>	Iraq	IPK
SPE-113/2	<i>Ae. 921/87</i>	Iraq	IPK
SPE-113/3	<i>Ae. 921/87</i>	Israel	IPK
SPE-114/1	<i>Ae. 1026/91</i>	Israel	IPK
SPE-114/2	<i>Ae. 1026/91</i>	Israel	IPK
SPE-114/3	<i>Ae. 1026/91</i>	Israel	IPK

<i>Aegilops</i> -No	Accession-No	Species	Origin	Source
SPE-115/1	AE 1063/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria	IPK
SPE-115/2	AE 1063/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria	IPK
SPE-115/3	AE 1063/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria	IPK
SPE-116/1	AE 1064/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria	IPK
SPE-116/3	AE 1064/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria	IPK
SPE-116/4	AE 1064/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria	IPK
SPE-117/2	AE 1065/95	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria	IPK
SPE-117/3	AE 1065/95	<i>Ae. speltoides</i>	Syria	IPK
SPE-118/1	AE 1066/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria	IPK
SPE-118/3	AE 1066/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria	IPK
SPE-118/4	AE 1066/92	<i>Ae. speltoides</i> subsp. <i>speltoides</i>	Syria	IPK
SEA-119/1	AE 1071/95	<i>Ae. speltoides</i>	Jordan	IPK
SEA-119/2	AE 1071/95	<i>Ae. speltoides</i>	Jordan	IPK
SEA-119/3	AE 1071/95	<i>Ae. speltoides</i>	Jordan	IPK
SEA-120/2	AE 1072/97	<i>Ae. speltoides</i>	Jordan	IPK
SEA-120/3	AE 1072/97	<i>Ae. speltoides</i>	Jordan	IPK
SEA-121/1	AE 1073/92	<i>Ae. searsii</i>	Jordan	IPK
SEA-121/2	AE 1073/92	<i>Ae. searsii</i>	Jordan	IPK
SEA-121/3	AE 1073/92	<i>Ae. searsii</i>	Jordan	IPK
SEA-122/2	AE 1074/93	<i>Ae. searsii</i>	Jordan	IPK
SEA-122/3	AE 1074/93	<i>Ae. searsii</i>	Jordan	IPK
SEA-123/1	AE 1075/95	<i>Ae. searsii</i>	Jordan	IPK
SEA-123/2	AE 1075/95	<i>Ae. searsii</i>	Jordan	IPK
SEA-123/3	AE 1075/95	<i>Ae. searsii</i>	Jordan	IPK
SEA-124/1	AE 1076/92	<i>Ae. searsii</i>	Jordan	IPK
SEA-124/2	AE 1076/92	<i>Ae. searsii</i>	Jordan	IPK
SEA-124/4	AE 1076/92	<i>Ae. searsii</i>	Jordan	IPK
SEA-124/5	AE 1076/92	<i>Ae. searsii</i>	Jordan	IPK
LOG-125/1	AE 1077/94	<i>Ae. longissima</i> subsp. <i>longissima</i>	Jordan	IPK
LOG-125/3	AE 1077/94	<i>Ae. longissima</i> subsp. <i>longissima</i>	Jordan	IPK
LOG-125/4	AE 1077/94	<i>Ae. longissima</i> subsp. <i>longissima</i>	Jordan	IPK
LOG-125/5	AE 1077/94	<i>Ae. longissima</i> subsp. <i>longissima</i>	Jordan	IPK
LOG-126/1	AE 1078/92	<i>Ae. longissima</i> subsp. <i>longissima</i>	Jordan	IPK
LOG-126/2	AE 1078/92	<i>Ae. longissima</i> subsp. <i>longissima</i>	Jordan	IPK
LOG-126/3	AE 1078/92	<i>Ae. longissima</i> subsp. <i>longissima</i>	Jordan	IPK
BIC-127/3	AE 1079/95	<i>Ae. bicarinis</i>	Jordan	IPK
BIC-127/5	AE 1079/95	<i>Ae. bicarinis</i>	Jordan	IPK
BIC-128/3	AE 1080/95	<i>Ae. bicarinis</i>	Syria	IPK
SEA-129/1	AE 1081/97	<i>Ae. searsii</i>	Syria	IPK
SEA-129/2	AE 1081/97	<i>Ae. searsii</i>	Syria	IPK
SEA-129/3	AE 1081/97	<i>Ae. searsii</i>	Syria	IPK
SEA-130/1	AE 1083/97	<i>Ae. searsii</i>	Syria	IPK
SEA-130/3	AE 1083/97	<i>Ae. searsii</i>	Syria	IPK
SEA-130/4	AE 1083/97	<i>Ae. searsii</i>	Syria	IPK

SPE-131/1	AE 1084/92	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Syria
SPE-131/2	AE 1084/92	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Syria
SPE-131/4	AE 1084/92	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Syria
SPE-132/1	AE 1085/92	<i>Ae. speltoides</i>	Syria
SPE-132/2	AE 1085/92	<i>Ae. speltoides</i>	Syria
SPE-132/3	AE 1085/92	<i>Ae. speltoides</i>	Syria
SPE-133/1	AE 1086/92	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Syria
SPE-133/2	AE 1086/92	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Syria
SPE-133/4	AE 1086/92	<i>Ae. speltoides</i> subsp. <i>speltooides</i>	Syria
SHA-134/1	AE 1203/97	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel
SHA-134/2	AE 1203/97	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel
SHA-134/3	AE 1203/97	<i>Ae. longissima</i> subsp. <i>longissima</i>	Israel
BIC-135/1	Clae 47	<i>Ae. bicarinis</i>	unknown
BIC-135/2	Clae 47	<i>Ae. bicarinis</i>	unknown
BIC-135/3	Clae 47	<i>Ae. bicarinis</i>	unknown
BIC-135/4	Clae 47	<i>Ae. bicarinis</i>	unknown
BIC-136/1	Clae 70	<i>Ae. bicarinis</i>	unknown
BIC-136/2	Clae 70	<i>Ae. bicarinis</i>	unknown
BIC-136/3	Clae 70	<i>Ae. bicarinis</i>	unknown
LOG-137/1	PI 1330486	<i>Ae. longissima</i>	unknown
LOG-137/2	PI 1330486	<i>Ae. longissima</i>	unknown
LOG-137/3	PI 1330486	<i>Ae. longissima</i>	unknown
LOG-138/1	PI 542196	<i>Ae. longissima</i>	Turkey, Izmir
LOG-138/2	PI 542196	<i>Ae. longissima</i>	Turkey, Izmir
LOG-138/3	PI 542196	<i>Ae. longissima</i>	Turkey, Izmir
LOG-139/2	PI 604103	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-139/4	PI 604103	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-139/5	PI 604103	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-140/1	PI 604104	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-140/2	PI 604104	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-140/3	PI 604104	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-142/1	PI 604106	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-142/2	PI 604106	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-142/3	PI 604106	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-143/3	PI 604107	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-143/5	PI 604107	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-144/1	PI 604108	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-144/2	PI 604108	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-144/3	PI 604108	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-145/2	PI 604109	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-145/3	PI 604109	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-147/1	PI 604111	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-147/2	PI 604111	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-147/3	PI 604111	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-148/2	PI 604112	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E
LOG-148/3	PI 604112	<i>Ae. longissima</i>	Israel, Shedema, 31°50' N, 34°44' E

<i>Aegilops</i> -No	Accession-No	Species	Origin	Source
SEA-181/1	PI 599125	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-181/2	PI 599125	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-181/4	PI 599125	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-182/1	PI 599126	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-182/2	PI 599126	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-182/3	PI 599126	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-183/1	PI 599128	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-183/2	PI 599128	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-183/3	PI 599128	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-184/1	PI 599129	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-184/2	PI 599129	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-184/5	PI 599129	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-185/1	PI 599130	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-185/2	PI 599130	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-185/4	PI 599130	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-186/1	PI 599131	<i>Ae. searsii</i>	Israel, Kokav haShahar, 31°58'N, 35°20'E	USDA
SEA-186/3	PI 599131	<i>Ae. searsii</i>	Jordan, Tumeira, 32° 23'N, 35°59'E	USDA
SEA-186/4	PI 599131	<i>Ae. searsii</i>	Jordan, Tumeira, 32° 23'N, 35°59'E	USDA
SEA-187/1	PI 599132	<i>Ae. searsii</i>	Jordan, Tumeira, 32° 23'N, 35°59'E	USDA
SEA-187/2	PI 599132	<i>Ae. searsii</i>	Jordan, Tumeira, 32° 23'N, 35°59'E	USDA
SEA-187/3	PI 599132	<i>Ae. searsii</i>	Jordan, El Buweida, 32° 21'N, 36°2'E	USDA
SEA-188/1	PI 599133	<i>Ae. searsii</i>	Jordan, El Buweida, 32° 21'N, 36°2'E	USDA
SEA-188/2	PI 599133	<i>Ae. searsii</i>	Jordan, El Buweida, 32° 21'N, 36°2'E	USDA
SEA-188/3	PI 599133	<i>Ae. searsii</i>	Jordan, Haiyan er Ruweibid, 32°15'N; 36°37'E	USDA
SEA-189/1	PI 599134	<i>Ae. searsii</i>	Jordan, Haiyan er Ruweibid, 32°15'N; 36°37'E	USDA
SEA-189/2	PI 599134	<i>Ae. searsii</i>	Jordan, El Madwar, 32°17'N, 35°59'E	USDA
SEA-189/5	PI 599134	<i>Ae. searsii</i>	Jordan, El Madwar, 32°17'N, 35°59'E	USDA
SEA-190/1	PI 599135	<i>Ae. searsii</i>	Jordan, El Madwar, 32°17'N, 35°59'E	USDA
SEA-190/2	PI 599135	<i>Ae. searsii</i>	Jordan, Ballila, 32°22'N, 35°55'E	USDA
SEA-190/3	PI 599135	<i>Ae. searsii</i>	Jordan, Ballila, 32°22'N, 35°55'E	USDA
SEA-191/1	PI 599136	<i>Ae. searsii</i>	Jordan, Ballila, 32°22'N, 35°55'E	USDA
SEA-191/2	PI 599136	<i>Ae. searsii</i>	Jordan, Quaqqaqā, 32° 21'N, 35° 56'E	USDA
SEA-191/3	PI 599136	<i>Ae. searsii</i>	Jordan, Quaqqaqā, 32° 21'N, 35° 56'E	USDA
SEA-192/1	PI 599137	<i>Ae. searsii</i>	Jordan, Quaqqaqā, 32° 21'N, 35° 56'E	USDA
SEA-192/2	PI 599137	<i>Ae. searsii</i>	Jordan, between El-Mastaba ad Jubba, 32°10'N, 35°52'E	USDA
SEA-192/4	PI 599137	<i>Ae. searsii</i>	Jordan, between El-Mastaba ad Jubba, 32°10'N, 35°52'E	USDA
SEA-193/1	PI 599138	<i>Ae. searsii</i>	Jordan, between El-Mastaba ad Jubba, 32°10'N, 35°52'E	USDA
SEA-193/2	PI 599138	<i>Ae. searsii</i>	Jordan, Jureina, 31°46'N, 35°43'E	USDA
SEA-193/3	PI 599138	<i>Ae. searsii</i>	Jordan, Jureina, 31°46'N, 35°43'E	USDA
SEA-194/1	PI 599139	<i>Ae. searsii</i>	Jordan, Ibb, 31° 35'N, 35° 41'E	USDA
SEA-194/2	PI 599139	<i>Ae. searsii</i>	Jordan, Ibb, 31° 35'N, 35° 41'E	USDA
SEA-194/3	PI 599139	<i>Ae. searsii</i>	Jordan, Ibb, 31° 35'N, 35° 41'E	USDA
SEA-195/1	PI 599140	<i>Ae. searsii</i>	Jordan, Rashadiya, 30° 41'N, 35°45'E	USDA
SEA-195/2	PI 599140	<i>Ae. searsii</i>	Jordan, Rashadiya, 30° 41'N, 35°45'E	USDA

SEA-195/3	PI 599140	<i>Ae. searsii</i>	USDA
SEA-196/1	PI 599142	<i>Ae. searsii</i>	USDA
SEA-196/2	PI 599142	<i>Ae. searsii</i>	USDA
SEA-196/3	PI 599142	<i>Ae. searsii</i>	USDA
SEA-197/1	PI 599143	<i>Ae. searsii</i>	USDA
SEA-197/2	PI 599143	<i>Ae. searsii</i>	USDA
SEA-197/3	PI 599143	<i>Ae. searsii</i>	USDA
SEA-198/1	PI 599144	<i>Ae. searsii</i>	USDA
SEA-198/2	PI 599144	<i>Ae. searsii</i>	USDA
SEA-198/3	PI 599144	<i>Ae. searsii</i>	USDA
SEA-199/2	PI 599145	<i>Ae. searsii</i>	USDA
SEA-199/3	PI 599145	<i>Ae. searsii</i>	USDA
SEA-199/4	PI 599145	<i>Ae. searsii</i>	USDA
SEA-200/1	PI 599146	<i>Ae. searsii</i>	USDA
SEA-200/2	PI 599146	<i>Ae. searsii</i>	USDA
SEA-200/3	PI 599146	<i>Ae. searsii</i>	USDA
SEA-201/1	PI 599147	<i>Ae. searsii</i>	USDA
SEA-201/2	PI 599147	<i>Ae. searsii</i>	USDA
SEA-201/3	PI 599147	<i>Ae. searsii</i>	USDA
SEA-202/1	PI 599148	<i>Ae. searsii</i>	USDA
SEA-202/2	PI 599148	<i>Ae. searsii</i>	USDA
SEA-202/4	PI 599148	<i>Ae. searsii</i>	USDA
SEA-203/1	PI 599149	<i>Ae. searsii</i>	USDA
SEA-203/2	PI 599149	<i>Ae. searsii</i>	USDA
SEA-203/3	PI 599149	<i>Ae. searsii</i>	USDA
SEA-204/2	PI 599150	<i>Ae. searsii</i>	USDA
SEA-204/3	PI 599150	<i>Ae. searsii</i>	USDA
SEA-204/5	PI 599150	<i>Ae. searsii</i>	USDA
SEA-205/1	PI 599151	<i>Ae. searsii</i>	USDA
SEA-205/3	PI 599151	<i>Ae. searsii</i>	USDA
SEA-205/4	PI 599151	<i>Ae. searsii</i>	USDA
SEA-206/1	PI 599152	<i>Ae. searsii</i>	USDA
SEA-206/2	PI 599152	<i>Ae. searsii</i>	USDA
SEA-206/3	PI 599152	<i>Ae. searsii</i>	USDA
SEA-207/1	PI 599153	<i>Ae. searsii</i>	USDA
SEA-207/2	PI 599153	<i>Ae. searsii</i>	USDA
SEA-207/4	PI 599153	<i>Ae. searsii</i>	USDA
SEA-208/1	PI 599154	<i>Ae. searsii</i>	USDA
SEA-208/2	PI 599154	<i>Ae. searsii</i>	USDA
SEA-208/3	PI 599154	<i>Ae. searsii</i>	USDA
SEA-209/1	PI 599155	<i>Ae. searsii</i>	USDA
SEA-209/2	PI 599155	<i>Ae. searsii</i>	USDA
SEA-209/3	PI 599155	<i>Ae. searsii</i>	USDA
SEA-210/1	PI 599156	<i>Ae. searsii</i>	USDA
SEA-210/2	PI 599156	<i>Ae. searsii</i>	USDA
SEA-210/3	PI 599156	<i>Ae. searsii</i>	USDA
SEA-211/1	PI 599157	<i>Ae. searsii</i>	USDA
SEA-211/2	PI 599157	<i>Ae. searsii</i>	USDA
SEA-211/3	PI 599157	<i>Ae. searsii</i>	USDA

SEA-227/3	PI 599173	Ae. <i>searsii</i>	Israel, Yattir Forest, 31°21' N, 35°57' E
SEA-227/4	PI 599173	Ae. <i>searsii</i>	Israel, Yattir Forest, 31°21' N, 35°57' E
SEA-228/1	PI 599174	Ae. <i>searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E
SEA-228/3	PI 599174	Ae. <i>searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E
SEA-228/4	PI 599174	Ae. <i>searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E
SEA-229/1	PI 599175	Ae. <i>searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E
SEA-229/2	PI 599175	Ae. <i>searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E
SEA-229/3	PI 599175	Ae. <i>searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E
SEA-230/1	PI 599177	Ae. <i>searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E
SEA-230/2	PI 599177	Ae. <i>searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E
SEA-230/3	PI 599177	Ae. <i>searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E
SEA-230/4	PI 599177	Ae. <i>searsii</i>	Israel, Kokav haShahar, 31°58' N, 35°20' E
LOG-231/3	Clae 32	Ae. <i>sharonensis</i>	Unknown
LOG-231/4	Clae 32	Ae. <i>sharonensis</i>	Unknown
LOG-231/5	PI 542237	Ae. <i>sharonensis</i>	Turkey, Izmir
SHA-232/1	PI 542237	Ae. <i>sharonensis</i>	Turkey, Izmir
SHA-232/2	PI 542237	Ae. <i>sharonensis</i>	Turkey, Izmir
SHA-233/2	PI 584345	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-233/3	PI 584345	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-233/4	PI 584345	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-234/1	PI 584346	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-234/2	PI 584346	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-234/4	PI 584346	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-235/1	PI 584347	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-235/2	PI 584347	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-235/3	PI 584347	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-235/4	PI 584347	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-236/1	PI 584348	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-236/2	PI 584348	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-236/3	PI 584348	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-237/1	PI 584349	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-235/4	PI 584349	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-237/2	PI 584349	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-237/3	PI 584349	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-238/2	PI 584349	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-238/5	PI 584350	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-239/1	PI 584357	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-239/2	PI 584357	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-239/3	PI 584357	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-240/1	PI 584358	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-240/2	PI 584358	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-240/3	PI 584358	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-241/1	PI 584359	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-241/2	PI 584359	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-241/3	PI 584359	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-242/1	PI 584360	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-242/2	PI 584360	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E
SHA-242/3	PI 584360	Ae. <i>sharonensis</i>	Israel, Ben-Zakay I, 31°51' N, 34°43' E

<i>Aegilops</i> -No	Accession-No	Species	Origin	Source
SHA-306/2	PI 584430	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-306/3	PI 584430	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-307/1	PI 584431	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-307/3	PI 584431	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-307/4	PI 584431	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-308/1	PI 584432	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-308/2	PI 584432	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-308/4	PI 584432	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-308/5	PI 584432	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-309/1	PI 584433	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-309/2	PI 584433	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-309/3	PI 584433	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-310/2	PI 584434	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-310/3	PI 584434	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-310/4	PI 584434	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-311/1	PI 584435	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-311/2	PI 584435	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-311/3	PI 584435	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-312/1	PI 584436	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-312/2	PI 584436	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-312/3	PI 584436	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-313/1	PI 584437	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-313/2	PI 584437	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-313/3	PI 584437	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-314/1	PI 584438	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-314/2	PI 584438	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
SHA-314/3	PI 584438	<i>Ae. sharonensis</i>	Israel, Palmahim I, 31°55'N, 34°42'E	USDA
BIC-315/1	Clae 64	<i>Ae. speltoides</i>	Unknown	USDA
BIC-315/2	Clae 64	<i>Ae. speltoides</i>	Unknown	USDA
BIC-315/3	PI 170203	<i>Ae. speltoides</i>	Turkey, Kirkkareli, 41°20'N, 27°29'E	USDA
SPE-316/1	PI 170203	<i>Ae. speltoides</i>	Turkey, Kirkkareli, 41°20'N, 27°29'E	USDA
SPE-316/2	PI 170203	<i>Ae. speltoides</i>	Turkey, Kirkkareli, 41°20'N, 27°29'E	USDA
SPE-316/3	PI 170203	<i>Ae. speltoides</i>	Turkey, Kirkkareli, 41°20'N, 27°29'E	USDA
SPE-317/1	PI 170204	<i>Ae. speltoides</i>	Turkey, Kirkkareli, 41°20'N, 27°29'E	USDA
SPE-317/2	PI 170204	<i>Ae. speltoides</i>	Turkey, Kirkkareli, 41°20'N, 27°29'E	USDA
SPE-318/2	PI 172685	<i>Ae. speltoides</i>	Turkey, Diyarbakir, 37°55'N, 40°14'E	USDA
SPE-318/4	PI 172685	<i>Ae. speltoides</i>	Turkey, Diyarbakir, 37°55'N, 40°14'E	USDA
SPE-319/2	PI 173614	<i>Ae. speltoides</i>	Turkey, Sirt, 38°33'N, 41°45'E	USDA
SPE-319/5	PI 173614	<i>Ae. speltoides</i>	Turkey, Sirt, 38°33'N, 41°45'E	USDA
SPE-320/2	PI 174010	<i>Ae. speltoides</i>	Turkey, Diyarbakir, 37°55'N, 40°16'E	USDA
SPE-320/3	PI 174010	<i>Ae. speltoides</i>	Turkey, Diyarbakir, 37°55'N, 40°16'E	USDA
SPE-320/4	PI 174010	<i>Ae. speltoides</i>	Turkey, Diyarbakir, 37°55'N, 40°16'E	USDA
SPE-321/1	PI 219867	<i>Ae. speltoides</i>	Iraq, Salahadin, 36°24'N, 44°8'E	USDA
SPE-321/2	PI 219867	<i>Ae. speltoides</i>	Iraq, Salahadin, 36°24'N, 44°8'E	USDA

SHA-288/1		Israel, Hefzi-Bah, 32° 28' N, 34° 53' E	USDA
SHA-288/2	PI 584412	Israel, Hefzi-Bah, 32° 28' N, 34° 53' E	USDA
SHA-288/3	PI 584412	Israel, Hefzi-Bah, 32° 28' N, 34° 53' E	USDA
SHA-289/1	PI 584413	Israel, Hefzi-Bah, 32° 28' N, 34° 53' E	USDA
SHA-289/2	PI 584413	Israel, Hefzi-Bah, 32° 28' N, 34° 53' E	USDA
SHA-289/3	PI 584413	Israel, Hefzi-Bah, 32° 28' N, 34° 53' E	USDA
SHA-290/1	PI 584414	Israel, Ashdad, 31° 49' N, 34° 40' E	USDA
SHA-290/2	PI 584414	Israel, Ashdad, 31° 49' N, 34° 40' E	USDA
SHA-290/3	PI 584414	Israel, Ashdad, 31° 49' N, 34° 40' E	USDA
SHA-291/1	PI 584415	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-291/2	PI 584415	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-291/4	PI 584415	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-292/1	PI 584416	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-292/2	PI 584416	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-292/3	PI 584416	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-293/1	PI 584417	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-293/2	PI 584417	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-293/3	PI 584417	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-294/1	PI 584418	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-294/3	PI 584418	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SHA-294/4	PI 584418	Israel, Palmahim I, 31° 55' N, 34° 42' E	USDA
SPE-328/1	PI 449339	Turkey, 39° 0' N, 35° 0' E	USDA
SPE-328/2	PI 449339	Turkey, 39° 0' N, 35° 0' E	USDA
SPE-328/3	PI 449339	Turkey, 39° 0' N, 35° 0' E	USDA
SPE-329/1	PI 449340	Turkey, 39° 0' N, 35° 0' E	USDA
SPE-329/2	PI 449340	Turkey, 39° 0' N, 35° 0' E	USDA
SPE-329/5	PI 449340	Turkey, 39° 0' N, 35° 0' E	USDA
SPE-330/1	PI 486262	Turkey, 25 km SW Elazig, 38° 32' N, 39° 2' E	USDA
SPE-330/2	PI 486262	Turkey, 25 km SW Elazig, 38° 32' N, 39° 2' E	USDA
SPE-330/3	PI 486262	Turkey, 25 km SW Elazig, 38° 32' N, 39° 2' E	USDA
SPE-331/2	PI 486263	Turkey, Diyarbakir, 37° 58' N, 40° 20' E	USDA
SPE-331/3	PI 486263	Turkey, Diyarbakir, 37° 58' N, 40° 20' E	USDA
SPE-331/4	PI 486263	Turkey, Diyarbakir, 37° 58' N, 40° 20' E	USDA
SPE-332/1	PI 486264	Turkey, Diyarbakir, 37° 58' N, 40° 20' E	USDA
SPE-332/2	PI 486264	Turkey, Diyarbakir, 37° 58' N, 40° 20' E	USDA
SPE-332/3	PI 486264	Turkey, Diyarbakir, 37° 58' N, 40° 20' E	USDA
SPE-333/1	PI 487231	Syria, Aleppo, 36° 10' N, 36° 50' E	USDA
SPE-333/2	PI 487231	Syria, Aleppo, 36° 10' N, 36° 50' E	USDA
SPE-333/3	PI 487231	Syria, Aleppo, 36° 10' N, 36° 50' E	USDA
SPE-334/1	PI 487232	Syria, Idlib, 36° 14' N, 36° 33' E	USDA
SPE-334/2	PI 487232	Syria, Idlib, 36° 14' N, 36° 33' E	USDA
SPE-334/3	PI 487232	Syria, Aleppo, 36° 10' N, 36° 50' E	USDA
SPE-335/1	PI 487233	Syria, Aleppo, 37° 0' N, 36° 41' E	USDA
SPE-335/2	PI 487233	Syria, Aleppo, 37° 0' N, 36° 41' E	USDA
SPE-335/3	PI 487233	Syria, Aleppo, 37° 0' N, 36° 41' E	USDA
SPE-336/1	PI 487235	Syria, Latakia, 35° 40' N, 35° 52' E	USDA
SPE-336/3	PI 487235	Syria, Latakia, 35° 40' N, 35° 52' E	USDA
SPE-336/5	PI 487235	Syria, Latakia, 35° 40' N, 35° 52' E	USDA
SPE-337/1	PI 487237	Syria, Latakia, 35° 53' N, 35° 48' E	USDA

<i>Aegilops</i> -No	Accession-No	Species	Origin	Source
SPE-237/3	PI 487237	<i>Ae. speloides</i>	Syria, Latakia, 35°53'N, 35°48'E	USDA
SPE-237/4	PI 487237	<i>Ae. speloides</i>	Syria, Latakia, 35°53'N, 35°48'E	USDA
SPE-238/1	PI 487238	<i>Ae. speloides</i>	Syria, Tartus, 35°7'N, 36°7'E	USDA
SPE-238/2	PI 487238	<i>Ae. speloides</i>	Syria, Tartus, 35°7'N, 36°7'E	USDA
SPE-238/3	PI 487238	<i>Ae. speloides</i>	Syria, Tartus, 35°7'N, 36°7'E	USDA
SPE-239/1	PI 499261	<i>Ae. speloides</i>	China, 35°0 N, 105°0 E	USDA
SPE-239/2	PI 499261	<i>Ae. speloides</i>	China, 35°0 N, 105°0 E	USDA
SPE-239/3	PI 499261	<i>Ae. speloides</i>	China, 35°0 N, 105°0 E	USDA
SPE-240/1	PI 542238	<i>Ae. speloides</i>	Turkey, Diyarbakir, 37°58'N, 40°20'E	USDA
SPE-240/2	PI 542238	<i>Ae. speloides</i>	Turkey, Diyarbakir, 37°58'N, 40°20'E	USDA
SPE-240/3	PI 542238	<i>Ae. speloides</i>	Turkey, Diyarbakir, 37°58'N, 40°20'E	USDA
SPE-241/2	PI 573448	<i>Ae. speloides</i>	Turkey, Cankiri, 40°31'N, 33°38'E	USDA
SPE-241/3	PI 573448	<i>Ae. speloides</i>	Turkey, Cankiri, 40°31'N, 33°38'E	USDA
SPE-241/5	PI 573448	<i>Ae. speloides</i>	Turkey, Cankiri, 40°31'N, 33°38'E	USDA
SPE-242/1	PI 573449	<i>Ae. speloides</i>	Turkey, Cankiri, 40°31'N, 33°38'E	USDA
SPE-242/2	PI 573449	<i>Ae. speloides</i>	Turkey, Cankiri, 40°31'N, 33°38'E	USDA
SPE-242/3	PI 573449	<i>Ae. speloides</i>	Turkey, Cankiri, 40°31'N, 33°38'E	USDA
SPE-243/1	PI 573450	<i>Ae. speloides</i>	Turkey, Ankara, 40°2'N, 32°55'E	USDA
SPE-243/2	PI 573450	<i>Ae. speloides</i>	Turkey, Ankara, 40°2'N, 32°55'E	USDA
SPE-243/4	PI 573450	<i>Ae. speloides</i>	Turkey, Ankara, 40°2'N, 32°55'E	USDA
SPE-244/1	PI 573452	<i>Ae. speloides</i>	Turkey, Ankara, 40°2'N, 32°55'E	USDA
SPE-244/2	PI 573452	<i>Ae. speloides</i>	Turkey, Ankara, 40°2'N, 32°55'E	USDA
SPE-244/3	PI 573452	<i>Ae. speloides</i>	Turkey, Ankara, 40°2'N, 32°55'E	USDA
SPE-245/1	PI 542245	<i>Ae. speloides</i> var. <i>ligustica</i>	Turkey, Urfa, 36°56'N, 38°55'E	USDA
SPE-245/2	PI 542245	<i>Ae. speloides</i> var. <i>ligustica</i>	Turkey, Urfa, 36°56'N, 38°55'E	USDA
SPE-245/3	PI 542245	<i>Ae. speloides</i> var. <i>ligustica</i>	Turkey, Urfa, 36°56'N, 38°55'E	USDA
SPE-246/1	PI 542256	<i>Ae. speloides</i> var. <i>ligustica</i>	Turkey, Adiyaman, 37°58'N, 38°37'E	USDA
SPE-246/5	PI 542256	<i>Ae. speloides</i> var. <i>ligustica</i>	Turkey, Adiyaman, 37°58'N, 38°37'E	USDA
SPE-247/1	PI 560527	<i>Ae. speloides</i> var. <i>ligustica</i>	Turkey, Mus, 38°49'N, 41°35'E	USDA
SPE-247/2	PI 560527	<i>Ae. speloides</i> var. <i>ligustica</i>	Turkey, Mus, 38°49'N, 41°35'E	USDA
SPE-247/3	PI 560527	<i>Ae. speloides</i> var. <i>ligustica</i>	Turkey, Mus, 38°49'N, 41°35'E	USDA
SPE-248/1	PI 560528	<i>Ae. speloides</i> var. <i>ligustica</i>	Turkey, Sirt, 37°45'N, 42°10'E	USDA
SPE-248/2	PI 560528	<i>Ae. speloides</i> var. <i>ligustica</i>	Turkey, Sirt, 37°45'N, 42°10'E	USDA
SPE-248/3	PI 560528	<i>Ae. speloides</i> var. <i>ligustica</i>	Turkey, Sirt, 37°45'N, 42°10'E	USDA
SPE-249/1	PI 542269	<i>Ae. speloides</i> var. <i>speloides</i>	Turkey, Gaziantep, 37°5'N, 37°24'E	USDA
SPE-249/3	PI 542269	<i>Ae. speloides</i> var. <i>speloides</i>	Turkey, Gaziantep, 37°5'N, 37°24'E	USDA
SPE-249/4	PI 542269	<i>Ae. speloides</i> var. <i>speloides</i>	Turkey, Gaziantep, 37°5'N, 37°24'E	USDA
SPE-250/1	PI 542273	<i>Ae. speloides</i> var. <i>speloides</i>	Turkey, Adiyaman, 37°40'N, 37°57'E	USDA
SPE-250/2	PI 542273	<i>Ae. speloides</i> var. <i>speloides</i>	Turkey, Adiyaman, 37°40'N, 37°57'E	USDA
SPE-250/3	PI 542273	<i>Ae. speloides</i> var. <i>speloides</i>	Turkey, Adiyaman, 37°40'N, 37°57'E	USDA
SPE-251/1	PI 542274	<i>Ae. speloides</i> var. <i>speloides</i>	Turkey, Adiyaman, 38°1'N, 38°31'E	USDA
SPE-251/2	PI 542274	<i>Ae. speloides</i> var. <i>speloides</i>	Turkey, Adiyaman, 38°1'N, 38°31'E	USDA
SPE-251/3	PI 542274	<i>Ae. speloides</i> var. <i>speloides</i>	Turkey, Adiyaman, 38°1'N, 38°31'E	USDA
SPE-252/2	PI 560530	<i>Ae. speloides</i> var. <i>speloides</i>	Turkey, Sturt, 38°4'N, 41°47'E	USDA

SPE-352/3		Turkey, Sirt, 38°4' N, 41°47'E	USDA
SPE-352/4		Turkey, Sirt, 38°4' N, 41°47'E	USDA
SPE-353/1		Turkey, Sirt, 37°45' N, 42°10'E	USDA
SPE-353/2		Turkey, Sirt, 37°45' N, 42°10'E	USDA
SPE-353/3		Turkey, Sirt, 37°45' N, 42°10'E	USDA
SPE-354/1		Turkey, Sirt, 37°56' N, 42°16'E	USDA
SPE-354/2		Turkey, Sirt, 37°56' N, 42°16'E	USDA
SPE-354/3		Turkey, Sirt, 37°56' N, 42°16'E	USDA
SPE-355/1		Turkey, Sirt, 37°56' N, 42°21'E	USDA
SPE-355/2		Turkey, Sirt, 37°56' N, 42°21'E	USDA
SPE-355/4		Turkey, Sirt, 37°56' N, 42°21'E	USDA
SHA-357/1	TA 2065	Turkey, Elazig, 16 km NW of Elazig	WGRC
SHA-357/2	TA 2065	Turkey, Elazig, 16 km NW of Elazig	WGRC
SHA-357/3	TA 2065	Turkey, Elazig, 16 km NW of Elazig	WGRC
SEA-358/1	TA 2343	Syria, Damascus, Suburbs of Ghabaghish	WGRC
SEA-358/2	TA 2343	Syria, Damascus, Suburbs of Ghabaghish	WGRC
SEA-358/3	TA 2343	Syria, Damascus, Suburbs of Ghabaghish	WGRC
SEA-358/4	TA 2343	Syria, Damascus, Suburbs of Ghabaghish	WGRC
SEA-359/2	TA 2353	Jordan, West Bank, Yattir, 4.5 km NE of the park watchman's house; 10-15 km SE of Hebron	WGRC
SEA-359/3	TA 2353	Jordan, West Bank, Yattir, 4.5 km NE of the park watchman's house; 10-15 km SE of Hebron	WGRC
LOG-360/1	TA 1912	Israel, 3 km SE of Rehovot	WGRC
LOG-360/2	TA 1912	Israel, 3 km SE of Rehovot	WGRC
LOG-360/3	TA 1912	Israel, 3 km SE of Rehovot	WGRC
LOG-361/1	TA 1921	Jordan, Al Balqa', Basin of the Jordan River, 32°24' N, 36°0'E	WGRC
LOG-361/2	TA 1921	Jordan, Al Balqa', Basin of the Jordan River, 32°24' N, 36°0'E	WGRC
LOG-361/3	TA 1921	Jordan, Al Balqa', Basin of the Jordan River, 32°24' N, 36°0'E	WGRC
BIC-362/1	TA 1945	Egypt, Marsa Matruh, 21 km W of Alexandria, 33°15' N, 29°40'E	WGRC
BIC-362/3	TA 1945	Egypt, Marsa Matruh, 21 km W of Alexandria, 33°15' N, 29°40'E	WGRC
BIC-362/4	TE 01	Egypt, Marsa Matruh, 21 km W of Alexandria, 33°15' N, 29°40'E	WGRC
SEA-364/1	SEA-364/2	Israel, Yattir, southern Judea	WIS
SEA-364/3	TE 01	Israel, Yattir, southern Judea	WIS
SEA-365/1	TE 07	Israel, Kufar Fajer, Judea	WIS
SEA-365/2	TE 07	Israel, Kufar Fajer, Judea	WIS
SEA-365/3	TE 07	Israel, Kufar Fajer, Judea	WIS
SEA-366/1	TE 08	Israel, South of Daharia, Hebron-BEER Sheva Road	WIS
SEA-366/2	TE 08	Israel, South of Daharia, Hebron-BEER Sheva Road	WIS
SEA-366/3	TE 08	Israel, South of Daharia, Hebron-BEER Sheva Road	WIS
SEA-367/1	TE 10	Israel, East of Taiyiba, Samaria	WIS
SEA-367/3	TE 10	Israel, East of Taiyiba, Samaria	WIS
SEA-367/5	TE 10	Israel, East of Taiyiba, Samaria	WIS
SEA-369/1	TE 16	Syria, Gabagib	WIS
SEA-369/2	TE 16	Syria, Gabagib	WIS
SEA-369/3	TE 16	Syria, Gabagib	WIS
SEA-370/1	TE 17	Syria, Ramtha	WIS
SEA-370/4	TE 17	Syria, Ramtha	WIS
SEA-371/1	TE 19	Syria, Gabagib	WIS
SEA-371/2	TE 19	Syria, Gabagib	WIS
SEA-371/3	TE 19	Syria, Gabagib	WIS

<i>Aegilops</i> -No	Accession-No	Species	Origin	Source
SEA-372/1	TE 25	<i>Ae. searsii</i>	Israel, East of Lahav, Southwestern Judea	WIS
SEA-372/2	TE 25	<i>Ae. searsii</i>	Israel, East of Lahav, Southwestern Judea	WIS
SEA-372/4	TE 25	<i>Ae. searsii</i>	Israel, East of Lahav, Southwestern Judea	WIS
SEA-373/1	TE 36	<i>Ae. searsii</i>	Syria (From Karl Hammer, #AEG643/85)	WIS
SEA-373/2	TE 36	<i>Ae. searsii</i>	Syria (From Karl Hammer, #AEG643/85)	WIS
SEA-373/3	TE 36	<i>Ae. searsii</i>	Syria (From Karl Hammer, #AEG643/85)	WIS
BIC-374/1	TB 01	<i>Ae. bicornis</i>	From Sears (P60-39=1)	WIS
BIC-374/2	TB 01	<i>Ae. bicornis</i>	From Sears (P60-39=1)	WIS
BIC-374/3	TB 01	<i>Ae. bicornis</i>	From Sears (P60-39=1)	WIS
BIC-375/2	TB 02	<i>Ae. bicornis</i>	Israel, East of Revivim-Gevulot-Magen intersectin, Western Negev	WIS
BIC-375/3	TB 02	<i>Ae. bicornis</i>	Israel, East of Revivim-Gevulot-Magen intersectin, Western Negev	WIS
BIC-375/5	TB 02	<i>Ae. bicornis</i>	Israel, East of Revivim-Gevulot-Magen intersectin, Western Negev	WIS
BIC-376/1	TB 05	<i>Ae. bicornis</i>	Egypt, Matruh	WIS
BIC-376/2	TB 05	<i>Ae. bicornis</i>	Egypt, Matruh	WIS
BIC-376/3	TB 05	<i>Ae. bicornis</i>	Egypt, Matruh	WIS
BIC-377/1	TB 07	<i>Ae. bicornis</i>	Egypt, West of Alexandria	WIS
BIC-377/2	TB 07	<i>Ae. bicornis</i>	Egypt, West of Alexandria	WIS
BIC-377/3	TB 07	<i>Ae. bicornis</i>	Egypt, West of Alexandria	WIS
BIC-378/1	TB 08	<i>Ae. bicornis</i>	Rafiah - El Arish Road, Northwestern Sinai	WIS
BIC-378/2	TB 08	<i>Ae. bicornis</i>	Rafiah - El Arish Road, Northwestern Sinai	WIS
BIC-378/3	TB 08	<i>Ae. bicornis</i>	Rafiah - El Arish Road, Northwestern Sinai	WIS
BIC-379/1	TB 10	<i>Ae. bicornis</i>	Israel, Ein -Yorkeam, Central Negev	WIS
BIC-379/2	TB 10	<i>Ae. bicornis</i>	Israel, Ein -Yorkeam, Central Negev	WIS
BIC-379/3	TB 10	<i>Ae. bicornis</i>	Israel, Ein -Yorkeam, Central Negev	WIS
BIC-380/1	TB 19	<i>Ae. bicornis</i>	Lybia (from Karl Hammer (#AE788/92))	WIS
BIC-380/2	TB 19	<i>Ae. bicornis</i>	Lybia (from Karl Hammer (#AE788/92))	WIS
BIC-380/3	TB 19	<i>Ae. bicornis</i>	Lybia (from Karl Hammer (#AE788/92))	WIS
SHA-381/1	TH 01	<i>Ae. sharonensis</i>	Israel, Caesarea, Coastal Plain	WIS
SHA-381/3	TH 01	<i>Ae. sharonensis</i>	Israel, Caesarea, Coastal Plain	WIS
SHA-381/5	TH 01	<i>Ae. sharonensis</i>	Israel, Caesarea, Coastal Plain	WIS
SHA-382/2	TH 02	<i>Ae. sharonensis</i>	Israel, Naaman salt-marsh, near Acre	WIS
SHA-382/3	TH 02	<i>Ae. sharonensis</i>	Israel, Naaman salt-marsh, near Acre	WIS
SHA-382/4	TH 02	<i>Ae. sharonensis</i>	Israel, Naaman salt-marsh, near Acre	WIS
SHA-383/1	TH 04	<i>Ae. sharonensis</i>	Israel, Rehovot, Coastal Plain	WIS
SHA-383/4	TH 04	<i>Ae. sharonensis</i>	Israel, Rehovot, Coastal Plain	WIS
SHA-383/5	TH 04	<i>Ae. sharonensis</i>	Israel, Rehovot, Coastal Plain	WIS
SHA-384/1	TH 11	<i>Ae. sharonensis</i>	Israel, North of Haifa	WIS
SHA-384/2	TH 11	<i>Ae. sharonensis</i>	Israel, North of Haifa	WIS
SHA-384/3	TH 11	<i>Ae. sharonensis</i>	Israel, North of Haifa	WIS
LOG-385-2	TL 01	<i>Ae. longissima</i>	Israel, Revivim, Central Negev	WIS
LOG-385-3	TL 01	<i>Ae. longissima</i>	Israel, Revivim, Central Negev	WIS
LOG-386/1	TL 03	<i>Ae. longissima</i>	Israel, Rehovot, Coastal plain	WIS
LOG-386/2	TL 03	<i>Ae. longissima</i>	Israel, Rehovot, Coastal plain	WIS
LOG-386/3	TL 03	<i>Ae. longissima</i>	Israel, Rehovot, Coastal plain	WIS

TL 05	LOG-388/1	Israel, Nahariyya-Rosh Hanikra Road, Western Galilee
TL 05	LOG-388/2	Israel, Nahariyya-Rosh Hanikra Road, Western Galilee
TL 05	LOG-388/4	Israel, Nahariyya-Rosh Hanikra Road, Western Galilee
TL 05	LOG-388/1	Israel, Hadera-Karkur Road, Coastal plain
TL 07	LOG-389/1	Israel, Hadera-Karkur Road, Coastal plain
TL 07	LOG-389/2	Israel, Hadera-Karkur Road, Coastal plain
TL 07	LOG-389/4	Israel, Hadera-Karkur Road, Coastal plain
TL 07	LOG-392/1	Israel, East of Ein Gev, East of the lake of Galilee
TL 37	LOG-392/2	Israel, East of Ein Gev, East of the lake of Galilee
TL 37	LOG-392/4	Israel, East of Ein Gev, East of the lake of Galilee
TS 01	SPE-393/2	Israel, East of Ashqelon, Southern Coastal Plain
TS 01	SPE-393/3	Israel, East of Ashqelon, Southern Coastal Plain
TS 02	SPE-394/1	Israel, Ein Ayyala, South of Haifa
TS 02	SPE-394/3	Israel, Ein Ayyala, South of Haifa
TS 02	SPE-394/5	Israel, Ein Ayyala, South of Haifa
TS 05	SPE-395/1	Israel, North Of Zichron-Yaqov
TS 05	SPE-395/2	Israel, North Of Zichron-Yaqov
TS 05	SPE-395/3	Israel, North Of Zichron-Yaqov
TS 05	SPE-396/1	Israel, Wadi Hilazon, Western Galilee
TS 05	SPE-396/2	Israel, Wadi Hilazon, Western Galilee
TS 05	SPE-396/3	Israel, Wadi Hilazon, Western Galilee
TS 41	SPE-397/2	East of Givat-Koah, Shefela, Israel
TS 41	SPE-397/3	East of Givat-Koah, Shefela, Israel
TS 43	SPE-397/4	East of Givat-Koah, Shefela, Israel
TS 43	SPE-398/1	Israel, Akhikhud Junction, Western Galilee
TS 100	SPE-398/2	Israel, Akhikhud Junction, Western Galilee
TS 100	SPE-398/3	Israel, Akhikhud Junction, Western Galilee
4 - 1	LOG-399/1	Israel, Herzlia
4 - 1	LOG-399/2	Israel, Herzlia
4 - 1	LOG-399/3	Jordan, 16 km E of Dead Sea
5752	LOG-400/3	Jordan, Basin of the Jordan river
5754	LOG-401/3	Israel, Gesher haZiw, N of Nahariyya
14621	LOG-402/1	Israel, Gesher haZiw, N of Nahariyya
14621	LOG-402/2	Israel, Gesher haZiw, N of Nahariyya
14621	LOG-402/3	Israel, Beit Hananya, N of Zikhrom Ya'aqov
14624	LOG-403/1	Israel, Beit Hananya, N of Zikhrom Ya'aqov
14624	LOG-403/2	Israel, Beit Hananya, N of Zikhrom Ya'aqov
14624	LOG-403/4	Israel, Rishon le Ziyon
14627	LOG-404/1	Israel, Netanya, S of haSharon
14627	LOG-404/2	Israel, Netanya, S of haSharon
14627	LOG-404/3	Israel, Netanya, S of haSharon
14629	LOG-405/2	Israel, Rishon le Ziyon
14629	LOG-405/3	Israel, Rishon le Ziyon
14629	LOG-405/4	Israel, Rishon le Ziyon
14632	LOG-406/1	Israel, Ziqim
14632	LOG-406/2	Israel, Ziqim
14632	LOG-406/3	Israel, Ziqim
14635	LOG-407/1	Israel, ca. 12km NW of Ze'elim, NE of Amni'oz
14635	LOG-407/2	Israel, ca. 12km NW of Ze'elim, NE of Amni'oz
14635	LOG-407/3	Israel, ca. 12km NW of Ze'elim, NE of Amni'oz

<i>Aegilops</i> -No	Accession-No	Species	Origin	Source
LOG-408/1	14638	<i>Ae. longissima</i>	Israel, ca. 8 km S of Qiryat Gat, S of Ahuzzam	Kyoto
LOG-408/3	14638	<i>Ae. longissima</i>	Israel, ca. 8 km S of Qiryat Gat, S of Ahuzzam	Kyoto
LOG-408/4	14638	<i>Ae. longissima</i>	Israel, ca. 8 km S of Qiryat Gat, S of Ahuzzam	Kyoto
LOG-409/1	14641	<i>Ae. longissima</i>	Israel, NE of Be'er Sheva	Kyoto
LOG-409/2	14641	<i>Ae. longissima</i>	Israel, NE of Be'er Sheva	Kyoto
LOG-409/4	14641	<i>Ae. longissima</i>	Israel, NE of Be'er Sheva	Kyoto
LOG-410/1	14644	<i>Ae. longissima</i>	Israel, SE of Dimona	Kyoto
LOG-410/4	14644	<i>Ae. longissima</i>	Israel, SE of Dimona	Kyoto
LOG-410/5	14644	<i>Ae. longissima</i>	Israel, SE of Dimona	Kyoto
LOG-411/2	14646	<i>Ae. longissima</i>	Israel, ca. 25 km S of Be'er Sheva, W of Mashabbim	Kyoto
LOG-411/3	14646	<i>Ae. longissima</i>	Israel, ca. 25 km S of Be'er Sheva, W of Mashabbim	Kyoto
LOG-411/5	14646	<i>Ae. longissima</i>	Israel, ca. 25 km S of Be'er Sheva, W of Mashabbim	Kyoto
LOG-412/3	14648	<i>Ae. longissima</i>	Israel, 6 km N of Mizpe Ramon	Kyoto
LOG-412/4	14648	<i>Ae. longissima</i>	Israel, 6 km N of Mizpe Ramon	Kyoto
SEA-413/1	4 - 6	<i>Ae. searsii</i>	Jordan, 13 km N of Hebron	Kyoto
SEA-413/2	4 - 6	<i>Ae. searsii</i>	Jordan, 13 km N of Hebron	Kyoto
SEA-413/5	4 - 6	<i>Ae. searsii</i>	Jordan, 13 km N of Hebron	Kyoto
SEA-414/1	4 - 7	<i>Ae. searsii</i>	Syria, Suburbs of Gabagib	Kyoto
SEA-414/2	4 - 7	<i>Ae. searsii</i>	Syria, Suburbs of Gabagib	Kyoto
SEA-414/4	4 - 7	<i>Ae. searsii</i>	Syria, Suburbs of Gabagib	Kyoto
SEA-415/2	5755	<i>Ae. searsii</i>	Syria, Suburbs of Ramtha	Kyoto
SEA-415/3	5755	<i>Ae. searsii</i>	Syria, Suburbs of Ramtha	Kyoto
SEA-414/1	5755	<i>Ae. searsii</i>	Syria, Suburbs of Ramtha	Kyoto
SEA-415/4	5755	<i>Ae. searsii</i>	Syria, Suburbs of Ramtha	Kyoto
SEA-415/5	5755	<i>Ae. searsii</i>	Syria, Suburbs of Ramtha	Kyoto
SEA-416/2	5756	<i>Ae. searsii</i>	Syria, Suburbs of Gabagib	Kyoto
SEA-416/3	5756	<i>Ae. searsii</i>	Syria, Suburbs of Gabagib	Kyoto
SEA-416/4	5756	<i>Ae. searsii</i>	Syria, Suburbs of Gabagib	Kyoto
SEA-417/2	5760	<i>Ae. searsii</i>	Syria, Suburbs of Gabagib	Kyoto
SEA-417/3	5760	<i>Ae. searsii</i>	Syria, Suburbs of Gabagib	Kyoto
SEA-418/1	6142	<i>Ae. searsii</i>	Jordan, 27 km before Jarash from Ramtha, Ibid; 32°27'N, 35°55'E	Kyoto
SEA-418/2	6142	<i>Ae. searsii</i>	Jordan, 27 km before Jarash from Ramtha, Ibid; 32°27'N, 35°55'E	Kyoto
SEA-418/3	6142	<i>Ae. searsii</i>	Jordan, 27 km before Jarash from Ramtha, Ibid; 32°27'N, 35°55'E	Kyoto
SEA-419/2	6143	<i>Ae. searsii</i>	Jordan, 13 km after Mafraq, Ibid; 32°18'N, 36°10'E	Kyoto
SEA-419/3	6143	<i>Ae. searsii</i>	Jordan, 13 km after Mafraq, Ibid; 32°18'N, 36°10'E	Kyoto
SEA-419/4	6143	<i>Ae. searsii</i>	Jordan, 13 km after Mafraq, Ibid; 32°18'N, 36°10'E	Kyoto
SEA-420/1	6144 A	<i>Ae. searsii</i>	Jordan, 6 km S of Madaba, Amman; 31°37'N, 35°48'E	Kyoto
SEA-421/1	6144 B	<i>Ae. searsii</i>	Jordan, 6 km S of Madaba, Amman; 31°37'N, 35°48'E	Kyoto
SEA-421/2	6144 B	<i>Ae. searsii</i>	Jordan, 20 km S of the junction Amman - Desert road; 31°37'N, 36°2'E	Kyoto
SEA-422/1	6145	<i>Ae. searsii</i>	Jordan, 20 km S of the junction Amman - Desert road; 31°37'N, 36°2'E	Kyoto
SEA-422/2	6145	<i>Ae. searsii</i>	Jordan, 20 km S of the junction Amman - Desert road; 31°37'N, 36°2'E	Kyoto
SEA-423/1	14651	<i>Ae. searsii</i>	Israel, Gittit, 9 km W of Massu'a	Kyoto
SEA-423/2	14651	<i>Ae. searsii</i>	Israel, Gittit, 9 km W of Massu'a	Kyoto
SEA-423/3	14651	<i>Ae. searsii</i>	Israel, Gittit, 9 km W of Massu'a	Kyoto

SEA-424/4	<i>Ae. searsii</i>	Israel, W of Kokhav haShahar
SEA-424/5	<i>Ae. searsii</i>	Israel, W of Kokhav haShahar
SEA-425/1	<i>Ae. searsii</i>	Israel, Kokhav haShahar
SEA-425/3	<i>Ae. searsii</i>	Israel, Kokhav haShahar
SEA-425/4	<i>Ae. searsii</i>	Israel, Kokhav haShahar
SEA-426/1	<i>Ae. searsii</i>	Israel, ca. 32 km NW of Jericho
SEA-426/2	<i>Ae. searsii</i>	Israel, ca. 32 km NW of Jericho
SEA-426/3	<i>Ae. searsii</i>	Israel, ca. 32 km NW of Jericho
SEA-427/1	<i>Ae. searsii</i>	Israel, 3 km E of Ma'ale Mikhmas
SEA-427/2	<i>Ae. searsii</i>	Israel, 3 km E of Ma'ale Mikhmas
SEA-427/3	<i>Ae. searsii</i>	Israel, 3 km E of Ma'ale Mikhmas
SEA-428/1	<i>Ae. searsii</i>	Israel, Mahane Yatir, NE of Be'er Sheva
SEA-428/2	<i>Ae. searsii</i>	Israel, Mahane Yatir, NE of Be'er Sheva
SEA-428/3	<i>Ae. searsii</i>	Israel, Mahane Yatir, NE of Be'er Sheva
SEA-429/1	<i>Ae. searsii</i>	Israel, N of Har anassa Nature Reserve, E of Mahane Yatir
SEA-429/3	<i>Ae. searsii</i>	Israel, N of Har anassa Nature Reserve, E of Mahane Yatir
SEA-429/4	<i>Ae. searsii</i>	Israel, N of Har anassa Nature Reserve, E of Mahane Yatir
SEA-430/1	<i>Ae. searsii</i>	Israel, NW of Arad, 8 km N of Tel Arad
SEA-430/2	<i>Ae. searsii</i>	Israel, NW of Arad, 8 km N of Tel Arad
SEA-430/3	<i>Ae. searsii</i>	Israel, NW of Arad, 8 km N of Tel Arad
SHA-431/2	<i>5 - 2</i>	Israel, near Cesarea, Sharon plain
SHA-431/2	<i>5 - 2</i>	Israel, near Cesarea, Sharon plain
SHA-431/3	<i>5 - 2</i>	Israel, near Cesarea, Sharon plain
SHA-432/1	<i>5 - 3</i>	Israel, near Maagan Michael
SHA-432/2	<i>5 - 3</i>	Israel, near Maagan Michael
SHA-432/4	<i>5 - 3</i>	Israel, near Maagan Michael
SHA-433/1	<i>14661</i>	Israel, Ein Hamifratz, S of Akko
SHA-433/2	<i>14661</i>	Israel, Ein Hamifratz, S of Akko
SHA-433/4	<i>14661</i>	Israel, Haifa, Qishon
SHA-434/1	<i>14662</i>	Israel, Haifa, Qishon
SHA-434/2	<i>14662</i>	Israel, Haifa, Qishon
SHA-434/3	<i>14662</i>	Israel, Haifa, Qishon
SHA-435/1	<i>14663</i>	Israel, haBonim
SHA-435/2	<i>14663</i>	Israel, haBonim
SHA-435/3	<i>14663</i>	Israel, haBonim
SHA-436/2	<i>14664</i>	Israel, Caesarea
SHA-436/4	<i>14664</i>	Israel, Caesarea
SHA-436/5	<i>14664</i>	Israel, Caesarea
SHA-437/1	<i>14665</i>	Israel, Caesarea
SHA-437/2	<i>14665</i>	Israel, Caesarea
SHA-437/3	<i>14665</i>	Israel, Caesarea
SHA-438/1	<i>14666</i>	Israel, NE of Giv'at Olga
SHA-438/2	<i>14666</i>	Israel, NE of Giv'at Olga
SHA-438/3	<i>14666</i>	Israel, NE of Giv'at Olga
SHA-439/1	<i>14667</i>	Israel, Mikhmoret, 10 km S of Hadera
SHA-439/2	<i>14667</i>	Israel, Mikhmoret, 10 km S of Hadera
SHA-439/3	<i>14667</i>	Israel, Mikhmoret, 10 km S of Hadera
SHA-439/4	<i>14667</i>	Israel, Wingate, S of Netanya
SHA-440/1	<i>14668</i>	

<i>Aegilops</i> -No	Accession-No	Species	Origin	Source
SHA-440/3	14668	<i>Ae. sharonensis</i>	Israel, Wingate, S of Netanya	Kyoto
SHA-440/5	14668	<i>Ae. sharonensis</i>	Israel, Wingate, S of Netanya	Kyoto
SHA-441/1	14669	<i>Ae. sharonensis</i>	Israel, Zahara, N of Tel Aviv	Kyoto
SHA-441/2	14669	<i>Ae. sharonensis</i>	Israel, Zahara, N of Tel Aviv	Kyoto
SHA-441/3	14669	<i>Ae. sharonensis</i>	Israel, Zahara, N of Tel Aviv	Kyoto
SHA-442/1	14670	<i>Ae. sharonensis</i>	Israel, near Soreq Nuclear Center	Kyoto
SHA-442/2	14670	<i>Ae. sharonensis</i>	Israel, near Soreq Nuclear Center	Kyoto
SHA-442/3	14670	<i>Ae. sharonensis</i>	Israel, near Soreq Nuclear Center	Kyoto
SHA-443/1	14671	<i>Ae. sharonensis</i>	Israel, N of Aashdod	Kyoto
SHA-443/2	14671	<i>Ae. sharonensis</i>	Israel, N of Aashdod	Kyoto
SHA-443/3	14671	<i>Ae. sharonensis</i>	Israel, N of Aashdod	Kyoto
SHA-444/3	14672	<i>Ae. sharonensis</i>	Israel, S of Ashqeron	Kyoto
SHA-444/4	14672	<i>Ae. sharonensis</i>	Israel, S of Ashqeron	Kyoto
SHA-445/1	14673	<i>Ae. sharonensis</i>	Israel, Ziqim	Kyoto
SHA-445/2	14673	<i>Ae. sharonensis</i>	Israel, Ziqim	Kyoto
SHA-445/3	14673	<i>Ae. sharonensis</i>	Israel, Ziqim	Kyoto
BIC-446/1	3 - 2	<i>Ae. bicornis</i>	Israel, 60 km W of Beer-Sheba	Kyoto
BIC-446/2	3 - 2	<i>Ae. bicornis</i>	Israel, 60 km W of Beer-Sheba	Kyoto
BIC-446/3	3 - 2	<i>Ae. bicornis</i>	Israel, 60 km W of Beer-Sheba	Kyoto
BIC-446/4	3 - 2	<i>Ae. bicornis</i>	Israel, 60 km W of Beer-Sheba	Kyoto
BIC-447/1	3 - 3	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-447/2	3 - 3	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-447/3	3 - 3	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-448/2	5782	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-448/3	5782	<i>Ae. bicornis</i>	Egypt, Matruh	Kyoto
BIC-449/2	5783	<i>Ae. bicornis</i>	Egypt, Matruh	Kyoto
BIC-449/3	5783	<i>Ae. bicornis</i>	Egypt, Matruh	Kyoto
BIC-451/1	5786	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-451/2	5786	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-451/3	5786	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-452/4	5787	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-452/5	5787	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-453/1	5788	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-453/3	5788	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-453/5	5788	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-455/2	5790	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-454/1	5790	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-454/2	5790	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-454/3	5790	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-455/1	5793	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-455/2	5793	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria	Kyoto
BIC-456/1	6141 A	<i>Ae. bicornis</i>	Jordan, 85 km NE of Aqaba; 29°55'E, 35°23'N	Kyoto
BIC-456/2	6141 A	<i>Ae. bicornis</i>	Jordan, 85 km NE of Aqaba; 29°55'E, 35°23'N	Kyoto
BIC-457/1	6141 B	<i>Ae. bicornis</i>	Jordan, 85 km NE of Aqaba; 29°55'E, 35°23'N	Kyoto
BIC-458/1	14610	<i>Ae. bicornis</i>	Israel, near Soreq Nuclear Center	Kyoto

BIC-458/2	<i>Ae. bicornis</i>	Israel, near Soreq Nuclear Center
BIC-458/4	<i>Ae. bicornis</i>	Israel, near Soreq Nuclear Center
BIC-459/1	<i>Ae. bicornis</i>	Israel, Nir Yizhaq
BIC-459/2	<i>Ae. bicornis</i>	Israel, Nir Yizhaq
BIC-459/3	<i>Ae. bicornis</i>	Israel, Nir Yizhaq
BIC-460/1	<i>Ae. bicornis</i>	Israel, roadside along Hwy 222 from Gevulot Junction to Gevulot
BIC-460/3	<i>Ae. bicornis</i>	Israel, roadside along Hwy 222 from Gevulot Junction to Gevulot
BIC-460/5	<i>Ae. bicornis</i>	Israel, roadside along Hwy 222 from Gevulot Junction to Gevulot
BIC-461/3	<i>Ae. bicornis</i>	Israel, Gevulot
BIC-461/4	<i>Ae. bicornis</i>	Israel, Gevulot
BIC-462/2	<i>Ae. bicornis</i>	Egypt, 40 km E from El Arish
BIC-462/3	<i>Ae. bicornis</i>	Egypt, 40 km E from El Arish
BIC-462/4	<i>Ae. bicornis</i>	Egypt, 40 km E from El Arish
BIC-463/1	<i>Ae. bicornis</i>	Egypt, Gamasa
BIC-463/2	<i>Ae. bicornis</i>	Egypt, Gamasa
BIC-463/3	<i>Ae. bicornis</i>	Egypt, Gamasa
BIC-464/2	<i>Ae. bicornis</i>	Egypt, Baltim
BIC-464/3	<i>Ae. bicornis</i>	Egypt, Baltim
BIC-464/4	<i>Ae. bicornis</i>	Egypt, Baltim
BIC-465/1	<i>Ae. bicornis</i>	Egypt, Baltim, eastside of the town
BIC-465/3	<i>Ae. bicornis</i>	Egypt, Baltim, eastside of the town
BIC-465/4	<i>Ae. bicornis</i>	Egypt, Baltim, eastside of the town
BIC-466/2	<i>Ae. bicornis</i>	Egypt, W of Rashid
BIC-466/3	<i>Ae. bicornis</i>	Egypt, W of Rashid
BIC-467/5	<i>Ae. bicornis</i>	Egypt, E of Alexandria
LOG-468/1	<i>Ae. longissima</i>	Israel, South of Yad-Mordekhai, Southern Coastal Plain
LOG-468/4	<i>Ae. longissima</i>	Israel, South of Yad-Mordekhai, Southern Coastal Plain
LOG-468/3	<i>Ae. longissima</i>	Israel, South of Yad-Mordekhai, Southern Coastal Plain
LOG-468/2	<i>Ae. longissima</i>	Israel, South of Yad-Mordekhai, Southern Coastal Plain
TAU-469/1	<i>Ae. tauschii</i>	Sanliurfa/Turkey
TAU-469/2	<i>Ae. tauschii</i>	Sanliurfa/Turkey
TAU-469/3	<i>Ae. tauschii</i>	Sanliurfa/Turkey
TAU-470/2	<i>Ae. tauschii</i>	Sanliurfa/Turkey
TAU-470/3	<i>Ae. tauschii</i>	Sanliurfa/Turkey
TAU-470/5	<i>Ae. tauschii</i>	Sanliurfa/Turkey
SPE-471/1	<i>Ae. speltooides</i>	Mersin/Mersin
SPE-471/2	<i>Ae. speltooides</i>	Mersin/Mersin
SPE-471/4	<i>Ae. speltooides</i>	Sanliurfa/Turkey
SPE-472/2	<i>Ae. speltooides</i>	Sanliurfa/Turkey
SPE-472/3	<i>Ae. speltooides</i>	Sanliurfa/Turkey
SPE-472/4	<i>Ae. speltooides</i>	Sanliurfa/Turkey
SPE-473/1	<i>Ae. speltooides</i>	Sanliurfa/Turkey
SPE-473/2	<i>Ae. speltooides</i>	Sanliurfa/Turkey
SPE-473/3	<i>Ae. speltooides</i>	Gaziantep/Turkey
SPE-474/1	<i>Ae. speltooides</i>	Gaziantep/Turkey
SPE-474/2	<i>Ae. speltooides</i>	Gaziantep/Turkey
SPE-474/3	<i>Ae. speltooides</i>	Adiyaman/Turkey
SPE-475/1	<i>Ae. speltooides</i>	Adiyaman/Turkey
SPE-475/2	<i>Ae. speltooides</i>	Adiyaman/Turkey

<i>Aegilops</i> -No	Accession-No	Species	Origin	Source
SPE-475/3	TUR 00623	<i>Ae. speltoides</i>	Adiyaman/Turkey	FCCRI
SPE-476/1	TUR 03355	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-476/2	TUR 03355	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-476/4	TUR 03355	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-477/1	TUR 03354	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-477/2	TUR 03354	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-477/3	TUR 03354	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-478/1	TUR 00903	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-478/2	TUR 00903	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-478/3	TUR 00903	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-479/1	TUR 02556	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-479/2	TUR 02556	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-479/3	TUR 02556	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-480/1	TUR 02774	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-481/1	TUR 01751	<i>Ae. speltoides</i>	Mardin/Turkey	FCCRI
SPE-481/2	TUR 01751	<i>Ae. speltoides</i>	Mardin/Turkey	FCCRI
SPE-481/3	TUR 01751	<i>Ae. speltoides</i>	Mardin/Turkey	FCCRI
SPE-482/1	TUR 00301	<i>Ae. speltoides</i>	Adiyaman/Turkey	FCCRI
SPE-482/2	TUR 00301	<i>Ae. speltoides</i>	Adiyaman/Turkey	FCCRI
SPE-482/3	TUR 00301	<i>Ae. speltoides</i>	Adiyaman/Turkey	FCCRI
SPE-483/1	TUR 03498	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-483/2	TUR 03498	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-483/4	TUR 03498	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-484/1	TUR 02764	<i>Ae. speltoides</i>	Adana/Turkey	FCCRI
SPE-484/2	TUR 02764	<i>Ae. speltoides</i>	Adana/Turkey	FCCRI
SPE-484/3	TUR 02764	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-485/1	TUR 01725	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-485/2	TUR 01725	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-485/3	TUR 01725	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-486/1	TUR 03425	<i>Ae. speltoides</i>	Hatay/Turkey	FCCRI
SPE-486/2	TUR 03425	<i>Ae. speltoides</i>	Hatay/Turkey	FCCRI
SPE-486/3	TUR 03425	<i>Ae. speltoides</i>	Hatay/Turkey	FCCRI
SPE-487/1	TUR 02592	<i>Ae. speltoides</i>	Gaziantep/Turkey	FCCRI
SPE-487/2	TUR 02592	<i>Ae. speltoides</i>	Gaziantep/Turkey	FCCRI
SPE-487/3	TUR 02592	<i>Ae. speltoides</i>	Gaziantep/Turkey	FCCRI
SPE-488/1	TUR 03374	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-488/2	TUR 03374	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-488/3	TUR 03374	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-489/1	TUR 03352	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-489/2	TUR 03352	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-489/3	TUR 03352	<i>Ae. speltoides</i>	Diyarbakir/Turkey	FCCRI
SPE-490/2	TUR 01191	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-490/1	TUR 01191	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI
SPE-490/3	TUR 01191	<i>Ae. speltoides</i>	Sanliurfa/Turkey	FCCRI

SPE-491/1	TUR 00488	<i>Ae. speltooides</i>	FCCRI
SPE-491/2	TUR 00488	<i>Ae. speltooides</i>	FCCRI
SPE-491/5	TUR 00488	<i>Ae. speltooides</i>	FCCRI
SPE-492/1	TUR 03384	<i>Ae. speltooides</i>	FCCRI
SPE-492/2	TUR 03384	<i>Ae. speltooides</i>	FCCRI
SPE-492/3	TUR 03384	<i>Ae. speltooides</i>	FCCRI
SPE-492/4	TUR 03384	<i>Ae. speltooides</i>	FCCRI
SPE-493/1	TUR 00634	<i>Ae. speltooides</i>	FCCRI
SPE-493/3	TUR 00634	<i>Ae. speltooides</i>	FCCRI
SPE-494/1	TUR 03416	<i>Ae. speltooides</i>	FCCRI
SPE-494/2	TUR 03416	<i>Ae. speltooides</i>	FCCRI
SPE-494/3	TUR 03416	<i>Ae. speltooides</i>	FCCRI
SPE-495/3	TUR 01765	<i>Ae. speltooides</i>	FCCRI
SPE-495/4	TUR 01765	<i>Ae. speltooides</i>	FCCRI
SPE-495/5	TUR 01765	<i>Ae. speltooides</i>	FCCRI
SPE-496/1	TUR 01642	<i>Ae. speltooides</i>	FCCRI
SPE-497/1	TUR 01690	<i>Ae. speltooides</i>	FCCRI
SPE-497/2	TUR 01690	<i>Ae. speltooides</i>	FCCRI
SPE-498/1	TUR 03287	<i>Ae. speltooides</i>	FCCRI
SPE-498/2	TUR 03287	<i>Ae. speltooides</i>	FCCRI
SPE-499/1	TUR 02210	<i>Ae. speltooides</i>	FCCRI
SPE-499/2	TUR 02210	<i>Ae. speltooides</i>	FCCRI
SPE-500/1	TUR 01689	<i>Ae. speltooides</i>	FCCRI
SPE-500/2	TUR 01689	<i>Ae. speltooides</i>	FCCRI
SPE-501/1	TUR 01636	<i>Ae. speltooides</i>	FCCRI
SPE-501/2	TUR 01636	<i>Ae. speltooides</i>	FCCRI

CHAPTER 4

Supplementary Table S3. List of the 850 unique lines selected among the 1372 lines in the initial screen

Amount input sequences total = 1372
 Amount unique sequences = 850
 Amount double sequences = 522

unique example	No	identical Lines
SPE-354/2	1	SPE-354/2
SPE-323/2	1	SPE-323/2
SPE-490/2	1	SPE-490/2
LOG-402/1	1	LOG-402/1
SHA-245/4	2	SHA-245/4 SHA-246/1
SPE-86/2	1	SPE-86/2
SPE-54/3	1	SPE-54/3
SPE-486/1	1	SPE-486/1
LOG-403/4	1	LOG-403/4
LOG-156/2	2	LOG-156/2 LOG-157/3
SHA-237/1	2	SHA-237/1 SHA-237/3
SPE-30/2	1	SPE-30/2
SPE-5/2	1	SPE-5/2
SPE-492/3	1	SPE-492/3
LOG-165/2	3	LOG-165/2 LOG-165/3 LOG-167/2
SPE-51/3	1	SPE-51/3
LOG-411/5	1	LOG-411/5
SPE-394/3	1	SPE-394/3
SPE-82/3	1	SPE-82/3
SPE-474/3	1	SPE-474/3
SPE-63/3	1	SPE-63/3
SPE-326/3	1	SPE-326/3
SPE-88/3	7	SPE-88/3 SPE-88/4 SPE-89/1 SPE-89/2 SPE-89/3 LOG-90/1 LOG-90/2
LOG-22/3	1	LOG-22/3
SPE-59/3	2	SPE-59/3 SPE-62/1
SPE-355/2	1	SPE-355/2
SHA-284/1	2	SHA-284/1 SHA-286/2
BIC-448/2	2	BIC-448/2 BIC-448/3
SHA-280/1	1	SHA-280/1
SPE-316/2	1	SPE-316/2
LOG-140/3	1	LOG-140/3
SPE-471/1	1	SPE-471/1
LOG-149/1	1	LOG-149/1
SEA-414/1	9	SEA-414/1 SEA-414/2 SEA-414/4 SEA-416/2 SEA-416/3 SEA-416/4 SEA-419/2 SEA-419/3 SEA-419/4
SPE-131/4	1	SPE-131/4
SPE-19/3	1	SPE-19/3
SPE-87/1	1	SPE-87/1
SPE-64/2	1	SPE-64/2
SHA-248/1	1	SHA-248/1
SPE-112/1	1	SPE-112/1
LOG-412/4	1	LOG-412/4
SEA-185/1	3	SEA-185/1 SEA-185/2 SEA-185/4
LOG-27/1	1	LOG-27/1
SPE-494/1	1	SPE-494/1
SHA-435/1	2	SHA-435/1 SHA-435/2
SPE-494/2	1	SPE-494/2
SHA-270/1	9	SHA-270/1 SHA-270/2 SHA-271/2 SHA-271/3 SHA-271/4 SHA-272/2 SHA-281/1 SHA-281/3 SHA-287/3
LOG-162/2	1	LOG-162/2
SHA-445/3	1	SHA-445/3
SPE-113/1	1	SPE-113/1
LOG-156/4	1	LOG-156/4
SPE-481/3	1	SPE-481/3
SHA-286/1	2	SHA-286/1 SHA-286/3
SPE-320/3	1	SPE-320/3
SPE-111/1	1	SPE-111/1
SPE-106/2	1	SPE-106/2
SPE-114/3	1	SPE-114/3
LOG-109/2	1	LOG-109/2

LOG-11/1	1	LOG-11/1
SPE-115/3	1	SPE-115/3
TAU-469/1	5	TAU-469/1 TAU-469/2 TAU-469/3 TAU-470/2 TAU-470/3
SEA-176/1	3	SEA-176/1 SEA-176/2 SEA-176/3
SPE-102/1	1	SPE-102/1
SPE-500/1	2	SPE-500/1 SPE-500/2
SPE-319/5	1	SPE-319/5
SPE-341/2	3	SPE-341/2 SPE-341/3 SPE-341/5
SEA-189/5	1	SEA-189/5
SPE-475/1	1	SPE-475/1
BIC-465/3	1	BIC-465/3
SHA-292/2	2	SHA-292/2 SHA-294/4
SPE-117/2	1	SPE-117/2
LOG-231/3	1	LOG-231/3
SPE-327/3	1	SPE-327/3
BIC-461/3	2	BIC-461/3 BIC-461/4
SHA-134/3	1	SHA-134/3
SHA-266/1	6	SHA-266/1 SHA-266/2 SHA-269/2 SHA-270/3 SHA-290/1 SHA-290/3
SHA-314/1	1	SHA-314/1
SHA-263/3	1	SHA-263/3
SPE-480/1	1	SPE-480/1
SPE-482/2	1	SPE-482/2
SHA-301/1	3	SHA-301/1 SHA-301/2 SHA-301/3
SHA-261/3	1	SHA-261/3
SPE-493/1	1	SPE-493/1
LOG-468/2	1	LOG-468/2
LOG-163/2	2	LOG-163/2 LOG-163/4
SPE-133/2	1	SPE-133/2
SHA-307/3	3	SHA-307/3 SHA-311/1 SHA-314/3
LOG-409/1	3	LOG-409/1 LOG-409/2 LOG-409/4
BIC-446/1	7	BIC-446/1 BIC-446/2 BIC-446/3 BIC-446/4 BIC-460/1 BIC-460/3 BIC-460/5
LOG-167/4	1	LOG-167/4
BIC-7/3	1	BIC-7/3
SPE-335/2	1	SPE-335/2
SHA-257/1	2	SHA-257/1 SHA-257/3
SPE-84/3	1	SPE-84/3
SPE-1/2	1	SPE-1/2
BIC-457/1	1	BIC-457/1
LOG-148/2	1	LOG-148/2
SPE-35/2	1	SPE-35/2
SEA-130/4	1	SEA-130/4
SEA-123/3	1	SEA-123/3
SPE-333/3	1	SPE-333/3
SHA-289/3	1	SHA-289/3
BIC-6/1	4	BIC-6/1 BIC-6/2 BIC-6/3 BIC-6/4
SPE-91/3	1	SPE-91/3
SEA-120/2	5	SEA-120/2 SEA-120/3 SEA-121/1 SEA-121/2 SEA-121/3
SHA-77/1	3	SHA-77/1 SHA-77/3 SHA-77/5
SEA-422/1	2	SEA-422/1 SEA-422/3
SHA-257/2	1	SHA-257/2
SEA-201/2	2	SEA-201/2 SEA-201/3
SPE-334/1	2	SPE-334/1 SPE-334/3
SHA-262/2	1	SHA-262/2
SHA-264/1	2	SHA-264/1 SHA-264/3
SEA-124/1	4	SEA-124/1 SEA-124/2 SEA-124/4 SEA-124/5
SPE-486/2	1	SPE-486/2
SPE-353/2	1	SPE-353/2
SPE-84/1	1	SPE-84/1
SHA-307/1	4	SHA-307/1 SHA-312/2 SHA-312/3 SHA-313/1
SPE-103/3	1	SPE-103/3
SPE-343/2	1	SPE-343/2
LOG-142/1	3	LOG-142/1 LOG-142/2 LOG-142/3
SEA-369/1	3	SEA-369/1 SEA-369/2 SEA-369/3
LOG-156/3	1	LOG-156/3
SPE-96/3	1	SPE-96/3
SPE-5/3	1	SPE-5/3
SPE-113/2	1	SPE-113/2
SHA-275/3	2	SHA-275/3 SHA-275/4
SHA-242/2	2	SHA-242/2 SHA-242/3
LOG-162/3	1	LOG-162/3
LOG-42/2	1	LOG-42/2
SPE-51/2	1	SPE-51/2
BIC-462/2	3	BIC-462/2 BIC-462/3 BIC-462/4
SPE-52/1	1	SPE-52/1
LOG-153/3	1	LOG-153/3
SPE-116/1	1	SPE-116/1

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unique example	No	identical Lines
SPE-30/1	1	SPE-30/1
BIC-466/2	2	BIC-466/2 BIC-466/3
LOG-165/1	1	LOG-165/1
SPE-354/3	1	SPE-354/3
LOG-231/4	1	LOG-231/4
LOG-125/1	6	LOG-125/1 LOG-125/4 LOG-125/5 LOG-126/1 LOG-126/2 LOG-126/3
SPE-81/3	1	SPE-81/3
SPE-33/2	1	SPE-33/2
LOG-386/1	3	LOG-386/1 LOG-386/2 LOG-386/3
SPE-349/1	1	SPE-349/1
SPE-115/2	1	SPE-115/2
BIC-447/1	3	BIC-447/1 BIC-447/2 BIC-447/3
SPE-316/1	1	SPE-316/1
SHA-300/3	1	SHA-300/3
SEA-202/1	3	SEA-202/1 SEA-202/2 SEA-202/4
BIC-127/5	1	BIC-127/5
SEA-205/1	1	SEA-205/1
SPE-478/1	1	SPE-478/1
SPE-476/4	1	SPE-476/4
SPE-331/4	1	SPE-331/4
SPE-395/3	1	SPE-395/3
SPE-18/3	1	SPE-18/3
SPE-83/4	1	SPE-83/4
LOG-8/3	1	LOG-8/3
SHA-277/1	2	SHA-277/1 SHA-277/2
SHA-134/1	2	SHA-134/1 SHA-134/2
SPE-473/2	1	SPE-473/2
SPE-111/2	1	SPE-111/2
SPE-337/1	1	SPE-337/1
SPE-483/4	1	SPE-483/4
BIC-451/1	3	BIC-451/1 BIC-451/2 BIC-451/3
SPE-324/3	1	SPE-324/3
SEA-189/1	2	SEA-189/1 SEA-189/2
SPE-118/1	1	SPE-118/1
SPE-479/3	2	SPE-479/3 SPE-481/2
LOG-71/2	1	LOG-71/2
SHA-436/5	1	SHA-436/5
SPE-351/1	1	SPE-351/1
SPE-56/4	1	SPE-56/4
SHA-260/2	2	SHA-260/2 SHA-260/3
SPE-79/3	2	SPE-79/3 SPE-80/1
SPE-347/1	1	SPE-347/1
SPE-48/2	1	SPE-48/2
SPE-84/2	1	SPE-84/2
SPE-65/1	1	SPE-65/1
SEA-372/4	1	SEA-372/4
SEA-97/1	2	SEA-97/1 SEA-97/2
SPE-93/3	1	SPE-93/3
LOG-167/3	1	LOG-167/3
SHA-285/1	1	SHA-285/1
SEA-98/2	1	SEA-98/2
BIC-7/4	1	BIC-7/4
SPE-132/1	1	SPE-132/1
SHA-444/3	2	SHA-444/3 SHA-444/4
LOG-148/3	1	LOG-148/3
SPE-340/3	1	SPE-340/3
SHA-259/1	1	SHA-259/1
LOG-9/1	1	LOG-9/1
SPE-335/3	1	SPE-335/3
SPE-487/1	1	SPE-487/1
BIC-378/1	3	BIC-378/1 BIC-378/2 BIC-378/3
SHA-252/1	1	SHA-252/1
LOG-28/2	1	LOG-28/2
SPE-321/1	2	SPE-321/1 SPE-321/1
SEA-427/1	2	SEA-427/1 SEA-427/2
SPE-85/2	1	SPE-85/2
SPE-3/2	1	SPE-3/2
LOG-147/3	1	LOG-147/3
BIC-449/2	2	BIC-449/2 BIC-449/3
SPE-133/4	1	SPE-133/4

SHA-246/3	1	SHA-246/3
SPE-48/4	1	SPE-48/4
SHA-442/1	1	SHA-442/1
SEA-119/1	1	SEA-119/1
SPE-20/3	1	SPE-20/3
SEA-217/2	32	SEA-217/2 SEA-218/1 SEA-218/2 SEA-218/3 SEA-219/1 SEA-219/2 SEA-219/3 SEA-220/1 SEA-220/2 SEA-220/3 SEA-221/1 SEA-221/2 SEA-221/3 SEA-221/4 SEA-222/2 SEA-222/3 SEA-223/1 SEA-223/2 SEA-223/3 SEA-224/1 SEA-224/2 SEA-224/3 SEA-225/2 SEA-225/3 SEA-226/1 SEA-227/2 SEA-227/3 SEA-227/4 SEA-230/1 SEA-230/2 SEA-230/3 SEA-230/4
SHA-94/2	1	SHA-94/2
BIC-374/1	3	BIC-374/1 BIC-374/2 BIC-374/3
SHA-262/1	1	SHA-262/1
LOG-12/4	1	LOG-12/4
SHA-294/3	1	SHA-294/3
SPE-113/3	1	SPE-113/3
LOG-74/4	1	LOG-74/4
SPE-80/3	1	SPE-80/3
SPE-61/1	1	SPE-61/1
SEA-365/1	6	SEA-365/1 SEA-365/2 SEA-365/3 SEA-366/1 SEA-366/2 SEA-366/3
SPE-92/4	1	SPE-92/4
LOG-154/1	3	LOG-154/1 LOG-154/2 LOG-154/4
LOG-147/1	2	LOG-147/1 LOG-147/2
BIC-465/1	2	BIC-465/1 BIC-465/4
SPE-66/3	1	SPE-66/3
SPE-66/2	1	SPE-66/2
SHA-291/1	1	SHA-291/1
SHA-435/3	1	SHA-435/3
SPE-497/1	1	SPE-497/1
SPE-346/5	1	SPE-346/5
SHA-252/2	2	SHA-252/2 SHA-253/4
SEA-415/2	6	SEA-415/2 SEA-415/3 SEA-415/4 SEA-415/5 SEA-417/2 SEA-417/3
LOG-385/2	2	LOG-385/2 LOG-385/3
SPE-325/2	1	SPE-325/2
LOG-169/3	1	LOG-169/3
SPE-481/1	1	SPE-481/1
SHA-253/2	1	SHA-253/2
SPE-348/3	1	SPE-348/3
BIC-315/2	2	BIC-315/2 BIC-315/3
SPE-55/4	1	SPE-55/4
SPE-483/2	1	SPE-483/2
SPE-394/1	2	SPE-394/1 SPE-394/5
SPE-326/1	1	SPE-326/1
SPE-317/1	1	SPE-317/1
SPE-60/3	1	SPE-60/3
BIC-458/1	3	BIC-458/1 BIC-458/2 BIC-458/4
SPE-489/3	1	SPE-489/3
SPE-111/3	1	SPE-111/3
SPE-397/3	2	SPE-397/3 SPE-397/4
LOG-388/1	2	LOG-388/1 LOG-388/4
BIC-127/3	1	BIC-127/3
SHA-23/5	1	SHA-23/5
SPE-355/1	1	SPE-355/1
SHA-13/3	1	SHA-13/3
SPE-53/3	2	SPE-53/3 SPE-53/5
SEA-426/1	3	SEA-426/1 SEA-426/2 SEA-426/3
LOG-27/3	1	LOG-27/3
BIC-105/3	1	BIC-105/3
LOG-139/5	1	LOG-139/5
SPE-131/1	1	SPE-131/1
SPE-491/5	1	SPE-491/5
SPE-483/1	1	SPE-483/1
LOG-410/1	3	LOG-410/1 LOG-410/4 LOG-410/5
LOG-403/1	2	LOG-403/1 LOG-403/2
SPE-349/4	1	SPE-349/4
SPE-57/3	1	SPE-57/3
SEA-130/1	1	SEA-130/1
LOG-9/4	1	LOG-9/4
SHA-263/1	2	SHA-263/1 SHA-263/2
SHA-445/1	2	SHA-445/1 SHA-445/2
SPE-67/4	1	SPE-67/4
LOG-149/2	1	LOG-149/2
LOG-138/1	3	LOG-138/1 LOG-138/2 LOG-138/3
SPE-79/2	1	SPE-79/2
LOG-405/3	1	LOG-405/3
SEA-359/2	3	SEA-359/2 SEA-372/1 SEA-372/2
SPE-486/3	2	SPE-486/3 SPE-501/1

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unique example	No	identical Lines
SHA-282/3	1	SHA-282/3
SPE-60/2	1	SPE-60/2
SPE-477/2	2	SPE-477/2 SPE-478/2
LOG-39/2	1	LOG-39/2
SPE-340/2	1	SPE-340/2
SPE-46/2	1	SPE-46/2
SHA-25/2	1	SHA-25/2
LOG-161/4	1	LOG-161/4
SPE-78/1	1	SPE-78/1
SPE-353/1	1	SPE-353/1
BIC-362/1	3	BIC-362/1 BIC-362/3 BIC-362/4
SPE-328/3	1	SPE-328/3
SPE-87/3	1	SPE-87/3
LOG-404/1	1	LOG-404/1
SHA-434/3	1	SHA-434/3
SPE-350/3	1	SPE-350/3
LOG-28/3	1	LOG-28/3
SHA-266/3	4	SHA-266/3 SHA-267/1 SHA-267/2 SHA-267/3
SHA-273/2	1	SHA-273/2
SEA-179/1	6	SEA-179/1 SEA-179/2 SEA-179/3 SEA-179/4 SEA-180/2 SEA-180/3
LOG-405/4	1	LOG-405/4
LOG-402/2	1	LOG-402/2
SPE-487/2	1	SPE-487/2
LOG-163/5	1	LOG-163/5
SPE-41/1	1	SPE-41/1
SHA-252/3	1	SHA-252/3
SEA-198/1	2	SEA-198/1 SEA-198/3
SHA-233/3	1	SHA-233/3
SPE-345/2	1	SPE-345/2
LOG-145/3	1	LOG-145/3
LOG-74/1	1	LOG-74/1
SEA-95/1	1	SEA-95/1
SPE-66/1	1	SPE-66/1
SPE-489/1	1	SPE-489/1
SPE-477/3	1	SPE-477/3
LOG-155/1	1	LOG-155/1
SHA-14/3	1	SHA-14/3
SPE-484/1	1	SPE-484/1
BIC-455/2	1	BIC-455/2
LOG-361/1	2	LOG-361/1 LOG-361/2
SEA-191/3	1	SEA-191/3
SPE-497/2	1	SPE-497/2
SHA-243/1	2	SHA-243/1 SHA-243/3
LOG-153/2	1	LOG-153/2
SHA-239/1	1	SHA-239/1
SPE-41/2	1	SPE-41/2
SHA-287/1	2	SHA-287/1 SHA-287/2
SPE-471/4	1	SPE-471/4
LOG-125/3	1	LOG-125/3
LOG-108/4	1	LOG-108/4
SPE-112/3	1	SPE-112/3
SHA-440/1	1	SHA-440/1
LOG-168/1	2	LOG-168/1 LOG-168/2
SPE-354/1	1	SPE-354/1
SHA-436/2	2	SHA-436/2 SHA-436/4
SPE-398/1	3	SPE-398/1 SPE-398/2 SPE-398/3
SHA-442/2	2	SHA-442/2 SHA-442/3
LOG-152/1	1	LOG-152/1
SPE-85/1	1	SPE-85/1
BIC-459/1	3	BIC-459/1 BIC-459/2 BIC-459/3
SHA-258/1	3	SHA-258/1 SHA-258/2 SHA-258/3
LOG-168/3	1	LOG-168/3
LOG-405/2	1	LOG-405/2
BIC-315/1	1	BIC-315/1
SHA-437/3	1	SHA-437/3
SPE-321/3	1	SPE-321/3
SEA-225/1	1	SEA-225/1
SPE-3/3	1	SPE-3/3
SHA-234/1	1	SHA-234/1
SEA-229/2	2	SEA-229/2 SEA-229/3

SHA-269/3	2	SHA-269/3 SHA-272/3
SPE-49/4	1	SPE-49/4
SPE-114/2	1	SPE-114/2
SPE-498/1	1	SPE-498/1
SHA-253/3	1	SHA-253/3
SPE-323/1	1	SPE-323/1
LOG-412/3	1	LOG-412/3
SPE-325/3	1	SPE-325/3
SHA-237/2	1	SHA-237/2
SPE-30/3	1	SPE-30/3
SEA-119/2	1	SEA-119/2
SHA-310/4	1	SHA-310/4
SPE-395/1	1	SPE-395/1
SHA-275/1	1	SHA-275/1
SHA-251/4	1	SHA-251/4
SPE-102/3	1	SPE-102/3
SPE-92/5	1	SPE-92/5
SPE-501/2	1	SPE-501/2
SPE-498/2	1	SPE-498/2
LOG-411/2	2	LOG-411/2 LOG-411/3
LOG-402/3	1	LOG-402/3
BIC-380/1	3	BIC-380/1 BIC-380/2 BIC-380/3
SHA-13/1	1	SHA-13/1
SPE-482/1	1	SPE-482/1
SPE-52/2	3	SPE-52/2 SPE-53/2 SPE-55/5
SPE-92/2	1	SPE-92/2
SPE-479/1	1	SPE-479/1
SPE-61/3	1	SPE-61/3
SPE-333/2	1	SPE-333/2
SHA-292/3	3	SHA-292/3 SHA-293/2 SHA-293/3
LOG-44/3	1	LOG-44/3
LOG-401/3	4	LOG-401/3 LOG-407/1 LOG-407/2 LOG-407/3
SPE-339/3	1	SPE-339/3
LOG-172/5	1	LOG-172/5
SPE-476/2	1	SPE-476/2
SPE-397/2	1	SPE-397/2
SPE-118/4	1	SPE-118/4
LOG-173/3	1	LOG-173/3
SEA-367/5	4	SEA-367/5 SEA-373/1 SEA-373/2 SEA-373/3
LOG-170/1	2	LOG-170/1 LOG-170/2
BIC-377/1	3	BIC-377/1 BIC-377/2 BIC-377/3
LOG-27/2	1	LOG-27/2
BIC-379/1	3	BIC-379/1 BIC-379/2 BIC-379/3
SPE-49/3	1	SPE-49/3
SPE-336/5	1	SPE-336/5
LOG-39/1	1	LOG-39/1
SPE-61/2	1	SPE-61/2
SPE-491/1	1	SPE-491/1
LOG-388/2	1	LOG-388/2
LOG-146/1	1	LOG-146/1
SPE-96/2	1	SPE-96/2
SPE-343/4	1	SPE-343/4
SPE-133/1	1	SPE-133/1
SPE-115/1	1	SPE-115/1
SPE-337/3	1	SPE-337/3
SPE-57/1	1	SPE-57/1
SHA-25/3	1	SHA-25/3
SEA-122/3	1	SEA-122/3
SPE-65/5	1	SPE-65/5
SPE-106/1	1	SPE-106/1
SPE-328/2	1	SPE-328/2
LOG-109/1	1	LOG-109/1
SPE-83/2	1	SPE-83/2
SPE-350/2	1	SPE-350/2
SPE-320/4	1	SPE-320/4
SHA-285/3	2	SHA-285/3 SHA-292/1
SHA-306/1	3	SHA-306/1 SHA-306/2 SHA-306/3
SPE-476/1	1	SPE-476/1
SPE-58/1	1	SPE-58/1
SHA-276/1	3	SHA-276/1 SHA-276/2 SHA-276/3
SPE-87/2	1	SPE-87/2
SPE-91/2	1	SPE-91/2
SHA-383/1	3	SHA-383/1 SHA-383/4 SHA-383/5
SPE-116/3	1	SPE-116/3
SHA-233/2	1	SHA-233/2
SPE-487/3	1	SPE-487/3

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unique example	No	identical Lines
SPE-31/1	1	SPE-31/1
SHA-250/1	1	SHA-250/1
LOG-153/1	1	LOG-153/1
BIC-464/2	3	BIC-464/2 BIC-464/3 BIC-464/4
SEA-198/2	1	SEA-198/2
LOG-45/3	1	LOG-45/3
SPE-495/4	1	SPE-495/4
LOG-159/1	1	LOG-159/1
LOG-171/1	1	LOG-171/1
SPE-56/1	2	SPE-56/1 SPE-58/4
LOG-71/1	1	LOG-71/1
BIC-455/1	1	BIC-455/1
SPE-328/1	1	SPE-328/1
SPE-76/3	1	SPE-76/3
SHA-274/3	2	SHA-274/3 SHA-290/2
SHA-433/1	4	SHA-433/1 SHA-433/2 SHA-433/4 SHA-434/2
SHA-235/3	3	SHA-235/3 SHA-236/1 SHA-236/2
SPE-327/4	1	SPE-327/4
SPE-484/2	1	SPE-484/2
LOG-160/1	1	LOG-160/1
SHA-304/3	1	SHA-304/3
SHA-294/1	1	SHA-294/1
SPE-112/2	1	SPE-112/2
SHA-254/2	3	SHA-254/2 SHA-259/2 SHA-295/2
LOG-360/1	3	LOG-360/1 LOG-360/2 LOG-360/3
SPE-353/3	1	SPE-353/3
SPE-491/2	2	SPE-491/2 SPE-494/3
SHA-285/2	1	SHA-285/2
SPE-350/1	1	SPE-350/1
SHA-431/2	3	SHA-431/2 SHA-431/2 SHA-431/3
LOG-408/1	3	LOG-408/1 LOG-408/3 LOG-408/4
SPE-343/1	1	SPE-343/1
SPE-334/2	1	SPE-334/2
SEA-193/2	5	SEA-193/2 SEA-193/3 SEA-194/1 SEA-194/2 SEA-194/3
SHA-382/3	1	SHA-382/3
LOG-137/1	3	LOG-137/1 LOG-137/2 LOG-137/3
SHA-443/1	3	SHA-443/1 SHA-443/2 SHA-443/3
LOG-155/2	1	LOG-155/2
SPE-344/2	1	SPE-344/2
BIC-467/5	1	BIC-467/5
LOG-175/2	1	LOG-175/2
SHA-94/1	1	SHA-94/1
SEA-425/1	3	SEA-425/1 SEA-425/3 SEA-425/4
BIC-105/1	1	BIC-105/1
SPE-114/1	1	SPE-114/1
LOG-157/1	1	LOG-157/1
LOG-9/3	1	LOG-9/3
SEA-95/2	2	SEA-95/2 SEA-95/3
BIC-105/2	1	BIC-105/2
LOG-45/2	1	LOG-45/2
SPE-79/1	1	SPE-79/1
SHA-295/3	1	SHA-295/3
SEA-187/1	1	SEA-187/1
SHA-240/1	3	SHA-240/1 SHA-240/2 SHA-240/3
SPE-339/2	1	SPE-339/2
SEA-129/1	2	SEA-129/1 SEA-129/3
SPE-317/2	1	SPE-317/2
LOG-389/1	3	LOG-389/1 LOG-389/2 LOG-389/4
SPE-490/3	1	SPE-490/3
SEA-423/1	3	SEA-423/1 SEA-423/2 SEA-423/3
SPE-57/2	1	SPE-57/2
LOG-161/1	1	LOG-161/1
SPE-396/1	1	SPE-396/1
SPE-338/1	1	SPE-338/1
SHA-16/1	2	SHA-16/1 SHA-16/2
SPE-41/3	1	SPE-41/3
SPE-54/2	1	SPE-54/2
SPE-2/2	1	SPE-2/2
SPE-347/2	1	SPE-347/2
SHA-288/1	3	SHA-288/1 SHA-288/2 SHA-288/3

SPE-34/1	1	SPE-34/1
LOG-400/3	1	LOG-400/3
SPE-319/2	1	SPE-319/2
SPE-396/3	1	SPE-396/3
SEA-359/3	1	SEA-359/3
SPE-50/3	1	SPE-50/3
SPE-76/4	1	SPE-76/4
SPE-472/4	1	SPE-472/4
SEA-420/1	3	SEA-420/1 SEA-421/1 SEA-421/2
SPE-86/1	1	SPE-86/1
SPE-329/1	2	SPE-329/1 SPE-329/2
LOG-43/3	1	LOG-43/3
SPE-49/1	1	SPE-49/1
LOG-74/2	1	LOG-74/2
SHA-241/1	2	SHA-241/1 SHA-241/2
SEA-180/4	4	SEA-180/4 SEA-183/1 SEA-183/2 SEA-183/3
LOG-173/2	1	LOG-173/2
SPE-56/2	1	SPE-56/2
SPE-101/1	1	SPE-101/1
SPE-106/3	1	SPE-106/3
LOG-151/2	1	LOG-151/2
SHA-300/2	1	SHA-300/2
BIC-453/1	3	BIC-453/1 BIC-453/3 BIC-453/5
SEA-190/3	1	SEA-190/3
LOG-44/2	1	LOG-44/2
SPE-316/3	1	SPE-316/3
SPE-116/4	1	SPE-116/4
SPE-322/3	1	SPE-322/3
LOG-40/2	1	LOG-40/2
SHA-439/1	3	SHA-439/1 SHA-439/2 SHA-439/3
SPE-17/4	1	SPE-17/4
SHA-438/1	3	SHA-438/1 SHA-438/2 SHA-438/3
SPE-330/3	1	SPE-330/3
BIC-454/1	3	BIC-454/1 BIC-454/2 BIC-454/3
SPE-21/3	1	SPE-21/3
SPE-495/3	2	SPE-495/3 SPE-495/5
LOG-109/3	1	LOG-109/3
SPE-3/1	1	SPE-3/1
SPE-493/3	1	SPE-493/3
LOG-146/2	2	LOG-146/2 LOG-146/3
SHA-265/3	1	SHA-265/3
SHA-296/1	2	SHA-296/1 SHA-298/3
LOG-140/1	1	LOG-140/1
BIC-376/1	3	BIC-376/1 BIC-376/2 BIC-376/3
SPE-344/3	1	SPE-344/3
SPE-58/3	1	SPE-58/3
LOG-399/1	3	LOG-399/1 LOG-399/2 LOG-399/3
SPE-5/1	1	SPE-5/1
SPE-488/1	1	SPE-488/1
SHA-289/1	2	SHA-289/1 SHA-289/2
LOG-175/3	1	LOG-175/3
SPE-62/5	1	SPE-62/5
SEA-187/2	2	SEA-187/2 SEA-187/3
SPE-54/1	1	SPE-54/1
SPE-32/5	1	SPE-32/5
SPE-479/2	1	SPE-479/2
SPE-19/1	1	SPE-19/1
LOG-108/1	1	LOG-108/1
SPE-492/2	2	SPE-492/2 SPE-496/1
SPE-78/3	1	SPE-78/3
SPE-104/1	1	SPE-104/1
LOG-144/2	1	LOG-144/2
SPE-325/1	1	SPE-325/1
LOG-160/3	1	LOG-160/3
SHA-382/4	1	SHA-382/4
SPE-488/3	1	SPE-488/3
SPE-34/3	1	SPE-34/3
SHA-308/5	1	SHA-308/5
SHA-234/2	2	SHA-234/2 SHA-239/2
SPE-333/1	1	SPE-333/1
SPE-67/2	1	SPE-67/2
SPE-338/2	1	SPE-338/2
SEA-413/1	3	SEA-413/1 SEA-413/2 SEA-413/5
SPE-32/2	1	SPE-32/2
BIC-452/4	2	BIC-452/4 BIC-452/5
SPE-318/2	1	SPE-318/2

unique example	No	identical Lines
SPE-489/2	1	SPE-489/2
SPE-355/4	1	SPE-355/4
SPE-131/2	1	SPE-131/2
SPE-477/1	1	SPE-477/1
SHA-272/1	1	SHA-272/1
LOG-169/2	1	LOG-169/2
SPE-50/4	1	SPE-50/4
SEA-229/1	1	SEA-229/1
LOG-392/2	2	LOG-392/2 LOG-392/4
LOG-149/3	1	LOG-149/3
SPE-472/3	1	SPE-472/3
SPE-4/3	1	SPE-4/3
SEA-193/1	1	SEA-193/1
SPE-339/1	1	SPE-339/1
LOG-145/2	1	LOG-145/2
SEA-192/1	3	SEA-192/1 SEA-192/2 SEA-192/4
LOG-361/3	1	LOG-361/3
SPE-336/1	2	SPE-336/1 SPE-336/3
SPE-482/3	1	SPE-482/3
SPE-59/1	1	SPE-59/1
SEA-422/2	1	SEA-422/2
SHA-247/1	3	SHA-247/1 SHA-247/2 SHA-247/3
SHA-440/3	1	SHA-440/3
SEA-181/1	9	SEA-181/1 SEA-181/2 SEA-181/4 SEA-182/1 SEA-182/2 SEA-182/3 SEA-184/1 SEA-184/2 SEA-184/5
SEA-119/3	3	SEA-119/3 SEA-123/1 SEA-123/2
SPE-393/2	2	SPE-393/2 SPE-393/3
SPE-485/3	1	SPE-485/3
SPE-342/1	1	SPE-342/1
SPE-55/2	1	SPE-55/2
BIC-135/1	7	BIC-135/1 BIC-135/2 BIC-135/3 BIC-135/4 BIC-136/1 BIC-136/2 BIC-136/3
SHA-273/1	6	SHA-273/1 SHA-273/3 SHA-281/2 SHA-282/1 SHA-291/2 SHA-291/4
SPE-101/2	1	SPE-101/2
SHA-235/1	7	SHA-235/1 SHA-235/2 SHA-235/4 SHA-236/3 SHA-242/1 SHA-242/4 SHA-243/2
LOG-173/1	2	LOG-173/1 LOG-173/5
SHA-381/3	2	SHA-381/3 SHA-381/5
SPE-46/3	1	SPE-46/3
SHA-296/2	1	SHA-296/2
SHA-284/3	1	SHA-284/3
SPE-82/1	1	SPE-82/1
SPE-345/1	2	SPE-345/1 SPE-345/3
SHA-274/1	2	SHA-274/1 SHA-274/2
LOG-40/5	1	LOG-40/5
SHA-303/1	3	SHA-303/1 SHA-305/1 SHA-305/2
SEA-191/1	2	SEA-191/1 SEA-191/2
LOG-152/2	1	LOG-152/2
SEA-122/2	1	SEA-122/2
SPE-322/2	1	SPE-322/2
SHA-262/3	1	SHA-262/3
SPE-35/1	1	SPE-35/1
SHA-245/1	2	SHA-245/1 SHA-245/2
SEA-424/4	2	SEA-424/4 SEA-424/5
SEA-418/1	3	SEA-418/1 SEA-418/2 SEA-418/3
LOG-140/2	1	LOG-140/2
LOG-169/1	1	LOG-169/1
SPE-473/1	1	SPE-473/1
SPE-51/1	1	SPE-51/1
SHA-232/2	2	SHA-232/2 SHA-232/2
SHA-268/1	3	SHA-268/1 SHA-268/2 SHA-268/3
SPE-488/2	1	SPE-488/2
SPE-395/2	1	SPE-395/2
SHA-249/2	2	SHA-249/2 SHA-249/3
SPE-485/2	1	SPE-485/2
SHA-248/3	1	SHA-248/3
SPE-478/3	1	SPE-478/3
SPE-48/1	1	SPE-48/1
SHA-308/2	4	SHA-308/2 SHA-309/1 SHA-313/2 SHA-313/3
SPE-338/3	1	SPE-338/3
LOG-392/1	1	LOG-392/1
SEA-428/1	9	SEA-428/1 SEA-428/2 SEA-428/3 SEA-429/1 SEA-429/3 SEA-429/4 SEA-430/1 SEA-430/2

		SEA-430/3
LOG-155/3	1	LOG-155/3
SEA-200/2	1	SEA-200/2
SHA-241/3	1	SHA-241/3
SPE-351/2	1	SPE-351/2
LOG-26/2	3	LOG-26/2 LOG-26/3 LOG-28/1
SHA-283/1	2	SHA-283/1 SHA-283/2
SHA-305/3	5	SHA-305/3 SHA-308/1 SHA-308/4 SHA-310/2 SHA-310/3
SPE-64/4	1	SPE-64/4
SHA-244/1	1	SHA-244/1
SHA-432/1	3	SHA-432/1 SHA-432/2 SHA-432/4
SPE-67/3	1	SPE-67/3
BIC-463/1	3	BIC-463/1 BIC-463/2 BIC-463/3
SEA-98/3	7	SEA-98/3 SEA-99/1 SEA-99/2 SEA-99/3 SEA-100/1 SEA-100/2 SEA-100/3
LOG-162/4	1	LOG-162/4
SEA-364/2	2	SEA-364/2 SEA-364/3
LOG-157/2	1	LOG-157/2
LOG-406/1	3	LOG-406/1 LOG-406/2 LOG-406/3
LOG-404/2	2	LOG-404/2 LOG-404/3
SPE-78/2	1	SPE-78/2
SPE-352/2	2	SPE-352/2 SPE-352/3
SPE-347/3	1	SPE-347/3
SPE-103/1	1	SPE-103/1
SHA-251/1	2	SHA-251/1 SHA-251/2
SPE-346/1	1	SPE-346/1
LOG-144/3	1	LOG-144/3
SHA-255/1	3	SHA-255/1 SHA-255/2 SHA-255/3
SHA-293/1	1	SHA-293/1
SHA-437/1	2	SHA-437/1 SHA-437/2
SPE-83/3	1	SPE-83/3
SHA-256/1	3	SHA-256/1 SHA-298/1 SHA-302/3
SPE-330/1	1	SPE-330/1
SPE-36/2	1	SPE-36/2
SPE-101/3	1	SPE-101/3
SPE-474/2	1	SPE-474/2
SPE-348/2	1	SPE-348/2
LOG-44/1	1	LOG-44/1
SPE-475/2	2	SPE-475/2 SPE-475/3
SPE-21/1	2	SPE-21/1 SPE-21/2
SEA-203/1	39	SEA-203/1 SEA-203/2 SEA-203/3 SEA-204/2 SEA-204/3 SEA-204/5 SEA-205/3 SEA-205/4 SEA-206/1 SEA-206/2 SEA-206/3 SEA-208/1 SEA-208/2 SEA-208/3 SEA-209/1 SEA-209/2 SEA-209/3 SEA-210/1 SEA-210/2 SEA-210/3 SEA-211/1 SEA-211/2 SEA-211/3 SEA-212/1 SEA-212/2 SEA-212/3 SEA-213/1 SEA-213/2 SEA-213/3 SEA-214/1 SEA-214/2 SEA-214/3 SEA-215/1 SEA-215/2 SEA-215/3 SEA-216/1 SEA-216/2 SEA-216/3 SEA-217/1
SPE-104/4	1	SPE-104/4
LOG-42/1	1	LOG-42/1
SPE-31/3	1	SPE-31/3
LOG-164/1	2	LOG-164/1 LOG-164/2
SHA-244/2	3	SHA-244/2 SHA-244/3 SHA-246/2
SPE-17/3	1	SPE-17/3
LOG-170/5	1	LOG-170/5
SHA-15/2	2	SHA-15/2 SHA-15/3
SEA-190/1	2	SEA-190/1 SEA-190/2
SPE-337/4	1	SPE-337/4
SPE-321/2	1	SPE-321/2
SEA-195/1	9	SEA-195/1 SEA-195/2 SEA-195/3 SEA-196/1 SEA-196/2 SEA-196/3 SEA-197/1 SEA-197/2 SEA-197/3
LOG-231/5	1	LOG-231/5
SHA-260/1	1	SHA-260/1
BIC-278/3	5	BIC-278/3 BIC-278/5 BIC-279/1 BIC-279/3 BIC-279/4
SPE-81/2	1	SPE-81/2
SPE-326/2	1	SPE-326/2
SHA-280/3	2	SHA-280/3 SHA-280/4
LOG-43/4	1	LOG-43/4
SEA-207/1	3	SEA-207/1 SEA-207/2 SEA-207/4
SHA-282/2	1	SHA-282/2
SEA-217/3	4	SEA-217/3 SEA-228/1 SEA-228/3 SEA-228/4
SHA-384/2	1	SHA-384/2
SHA-283/3	1	SHA-283/3
SHA-298/2	5	SHA-298/2 SHA-299/1 SHA-299/2 SHA-299/4 SHA-300/1
SPE-332/1	1	SPE-332/1
LOG-166/3	2	LOG-166/3 LOG-166/5
LOG-171/2	1	LOG-171/2
SPE-342/2	1	SPE-342/2
LOG-160/2	1	LOG-160/2
SHA-304/2	1	SHA-304/2

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unique example	No	identical Lines
SHA-239/3	1	SHA-239/3
SPE-324/2	1	SPE-324/2
SPE-50/1	1	SPE-50/1
SPE-1/4	1	SPE-1/4
SPE-93/2	1	SPE-93/2
SHA-16/3	1	SHA-16/3
SPE-349/3	1	SPE-349/3
SPE-327/1	1	SPE-327/1
SHA-233/4	1	SHA-233/4
LOG-71/3	1	LOG-71/3
BIC-375/2	3	BIC-375/2 BIC-375/3 BIC-375/5
SPE-88/2	1	SPE-88/2
SPE-332/3	1	SPE-332/3
SHA-277/4	1	SHA-277/4
SHA-303/2	2	SHA-303/2 SHA-304/1
SPE-331/3	1	SPE-331/3
LOG-159/2	1	LOG-159/2
SEA-98/1	1	SEA-98/1
SEA-177/1	6	SEA-177/1 SEA-177/2 SEA-177/3 SEA-178/1 SEA-178/2 SEA-178/3
LOG-108/3	1	LOG-108/3
SPE-118/3	1	SPE-118/3
LOG-43/1	1	LOG-43/1
SHA-269/4	2	SHA-269/4 SHA-284/2
SPE-36/3	1	SPE-36/3
SPE-132/2	1	SPE-132/2
SPE-472/2	1	SPE-472/2
SPE-323/3	1	SPE-323/3
SPE-499/2	1	SPE-499/2
LOG-139/4	1	LOG-139/4
SHA-234/4	1	SHA-234/4
SHA-14/1	2	SHA-14/1 SHA-14/2
SHA-249/1	3	SHA-249/1 SHA-250/2 SHA-250/3
SPE-18/2	1	SPE-18/2
LOG-143/3	2	LOG-143/3 LOG-144/1
SPE-92/1	1	SPE-92/1
SPE-82/2	1	SPE-82/2
SPE-492/4	1	SPE-492/4
SPE-342/3	1	SPE-342/3
SHA-259/3	1	SHA-259/3
SHA-357/1	3	SHA-357/1 SHA-357/2 SHA-357/3
SPE-85/3	1	SPE-85/3
SPE-474/1	1	SPE-474/1
SPE-20/2	1	SPE-20/2
SEA-186/1	6	SEA-186/1 SEA-186/3 SEA-186/4 SEA-188/1 SEA-188/2 SEA-188/3
SPE-329/5	1	SPE-329/5
SPE-96/1	1	SPE-96/1
SPE-33/4	1	SPE-33/4
LOG-26/1	1	LOG-26/1
SEA-358/1	9	SEA-358/1 SEA-358/2 SEA-358/3 SEA-358/4 SEA-370/1 SEA-370/4 SEA-371/1 SEA-371/2 SEA-371/3
SPE-132/3	1	SPE-132/3
SEA-364/1	1	SEA-364/1
SHA-384/1	2	SHA-384/1 SHA-384/3
LOG-42/4	1	LOG-42/4
SPE-64/1	1	SPE-64/1
SHA-265/2	1	SHA-265/2
SPE-63/2	1	SPE-63/2
SPE-1/3	1	SPE-1/3
LOG-150/1	3	LOG-150/1 LOG-150/2 LOG-150/4
SEA-130/3	1	SEA-130/3
SHA-434/1	1	SHA-434/1
SHA-256/2	1	SHA-256/2
SPE-471/2	1	SPE-471/2
LOG-45/1	1	LOG-45/1
SEA-367/1	2	SEA-367/1 SEA-367/3
SPE-91/1	1	SPE-91/1
LOG-174/1	3	LOG-174/1 LOG-174/2 LOG-174/4
SHA-261/2	1	SHA-261/2
SPE-490/1	1	SPE-490/1
SHA-110/2	1	SHA-110/2

SPE-59/2	1	SPE-59/2
SPE-335/1	1	SPE-335/1
SEA-97/3	1	SEA-97/3
SHA-381/1	1	SHA-381/1
SHA-238/2	2	SHA-238/2 SHA-238/5
BIC-128/3	1	BIC-128/3
SHA-248/2	1	SHA-248/2
SPE-473/3	1	SPE-473/3
SPE-348/1	1	SPE-348/1
SHA-254/1	5	SHA-254/1 SHA-254/3 SHA-297/1 SHA-297/2 SHA-297/3
SPE-318/4	1	SPE-318/4
BIC-456/1	2	BIC-456/1 BIC-456/2
SPE-485/1	1	SPE-485/1
SPE-31/2	1	SPE-31/2
SPE-36/1	1	SPE-36/1
SPE-352/4	1	SPE-352/4
SHA-261/1	1	SHA-261/1
SPE-340/1	1	SPE-340/1
SPE-52/3	1	SPE-52/3
SPE-492/1	2	SPE-492/1 SPE-499/1
SEA-427/3	1	SEA-427/3
SPE-351/3	1	SPE-351/3
SPE-103/2	1	SPE-103/2
LOG-143/5	2	LOG-143/5 LOG-159/3
SPE-330/2	1	SPE-330/2
SHA-264/2	1	SHA-264/2
SPE-20/1	1	SPE-20/1
SPE-344/1	1	SPE-344/1
SHA-307/4	5	SHA-307/4 SHA-311/2 SHA-311/3 SHA-312/1 SHA-314/2
SPE-396/2	1	SPE-396/2
SPE-76/1	1	SPE-76/1
LOG-175/4	1	LOG-175/4
LOG-22/1	1	LOG-22/1
SPE-2/1	3	SPE-2/1 SPE-2/3 SPE-4/4
LOG-151/3	1	LOG-151/3
LOG-161/2	1	LOG-161/2
SPE-80/2	2	SPE-80/2 SPE-86/3
LOG-164/3	1	LOG-164/3
SHA-309/2	2	SHA-309/2 SHA-309/3
LOG-468/1	3	LOG-468/1 LOG-468/4 LOG-468/3
SPE-17/2	1	SPE-17/2
LOG-172/1	1	LOG-172/1
SPE-117/3	1	SPE-117/3
TAU-470/5	1	TAU-470/5
SHA-382/2	1	SHA-382/2
SPE-19/2	1	SPE-19/2
LOG-11/2	1	LOG-11/2
SHA-303/3	1	SHA-303/3
SHA-295/1	1	SHA-295/1
SPE-484/3	1	SPE-484/3
SHA-296/3	1	SHA-296/3
SPE-93/1	1	SPE-93/1
SPE-332/2	1	SPE-332/2
SHA-302/1	2	SHA-302/1 SHA-302/2
LOG-151/1	1	LOG-151/1
BIC-7/2	1	BIC-7/2
SHA-256/3	1	SHA-256/3
SPE-34/2	1	SPE-34/2
SPE-320/2	1	SPE-320/2
SPE-81/1	1	SPE-81/1
SHA-439/4	1	SHA-439/4
LOG-139/2	1	LOG-139/2
SPE-104/2	1	SPE-104/2
LOG-152/4	1	LOG-152/4
SEA-129/2	1	SEA-129/2
SHA-232/1	1	SHA-232/1
LOG-39/3	1	LOG-39/3
SHA-440/5	4	SHA-440/5 SHA-441/1 SHA-441/2 SHA-441/3
LOG-171/3	1	LOG-171/3
SPE-331/2	1	SPE-331/2
SEA-199/2	6	SEA-199/2 SEA-199/3 SEA-199/4 SEA-200/1 SEA-200/3 SEA-201/1
SHA-110/1	1	SHA-110/1
SPE-324/1	1	SPE-324/1

Supplementary Table S4. List of the 94 lines analyzed in figure 3

Symbol	Short name	Accession-No	Species	Origin	Source
AES	CS	Chinese Spring	<i>T. aestivum</i> ssp. <i>aestivum</i>	Dr. B. Gill via Dr. E. Sears	WGRC
AES	Gonen		<i>T. aestivum</i> ssp. <i>aestivum</i>	Turkey	
AES	Panda		<i>T. aestivum</i> ssp. <i>aestivum</i>	Turkey	
AES	Bezostaya		<i>T. aestivum</i> ssp. <i>aestivum</i>	Turkey	
AES	Kirkpinar	AE Log42	<i>T. aestivum</i> ssp. <i>aestivum</i>	IPK	
LOG	Log126	AE 339/78	<i>Ae. longissima</i> ssp. <i>longissima</i>	IPK	
LOG	Log43	AE 340/84	<i>Ae. longissima</i> ssp. <i>longissima</i>	IPK	
LOG	Log137	AE 1078/92	<i>Ae. longissima</i> ssp. <i>longissima</i>	IPK	
LOG	Log150	PI 330486	<i>Ae. longissima</i>	USDA	
LOG	Log174	PI 604115	<i>Ae. longissima</i>	USDA	
LOG	Log399	PI 604143	<i>Ae. longissima</i>	USDA	
LOG	Log410	4 - 1	<i>Ae. longissima</i>	Kyoto	
SEA	Seal19	14644	<i>Ae. longissima</i>	Kyoto	
SEA	Seal19	AE 1071/95	<i>Ae. searsii</i>	IPK	
SEA	Seal21	AE 1073/92	<i>Ae. searsii</i>	IPK	
SEA	Seal23	AE 1075/95	<i>Ae. searsii</i>	IPK	
SEA	Seal24	AE 1076/92	<i>Ae. searsii</i>	IPK	
SEA	Seal84	PI 599129	<i>Ae. searsii</i>	IPK	
SEA	Seal87	PI 599132	<i>Ae. searsii</i>	IPK	
SEA	Seal96	PI 599142	<i>Ae. searsii</i>	IPK	
SEA	Sea211	PI 599157	<i>Ae. searsii</i>	IPK	
SEA	Sea223	PI 599169	<i>Ae. searsii</i>	IPK	
SEA	Sea365	TE 07	<i>Ae. searsii</i>	IPK	
SEA	Sea371	TE 19	<i>Ae. searsii</i>	IPK	
SEA	Sea427	14655	<i>Ae. searsii</i>	IPK	
SEA	Sea428	14656	<i>Ae. searsii</i>	IPK	
BIC	Bic6	AE 105/85	<i>Ae. bicornis</i> var. <i>bicornis</i>	IPK	
BIC	Bic136	Clae 70	<i>Ae. bicornis</i>	IPK	
BIC	Bic374	TB 01	<i>Ae. bicornis</i>	IPK	
BIC	Bic376	TB 05	<i>Ae. bicornis</i>	IPK	
BIC	Bic379	TB 10	<i>Ae. bicornis</i>	IPK	
BIC	Bic451	5786	<i>Ae. bicornis</i>	IPK	
BIC	Bic453	5788	<i>Ae. bicornis</i>	IPK	

BIC	Bic454	5790	<i>Ae. bicornis</i>	Kyoto
BIC	Bic460	14614 A	<i>Ae. bicornis</i>	Kyoto
BIC	Bic462	15002	<i>Ae. bicornis</i>	Egypt, 21 km W of Alexandria
BIC	Bic463	15004	<i>Ae. bicornis</i>	Israel, roadside along Hwy 222 from Gevulot
SHA	Shar110	AE 906/91	<i>Ae. longissima</i> ssp. <i>sharonensis</i>	Junction to Gevulot
SHA	Shar154	PI 604121	<i>Ae. longissima</i>	Egypt, 40 km E from El Arish
SHA	Shar253	PI 584371	<i>Ae. sharonensis</i>	Egypt, Gamasa
SHA	Shar255	PI 584374	<i>Ae. sharonensis</i>	Israel
SHA	Shar275	PI 584397	<i>Ae. sharonensis</i>	Beit-Lid; 32°19'N, 34°54'E
SHA	Shar286	PI 584409	<i>Ae. sharonensis</i>	Israel, Hefzi-Bah; 32°28'N, 34°53'E
SHA	Shar293	PI 584417	<i>Ae. sharonensis</i>	Israel, Hezzi-Bah; 32°28'N, 34°53'E
SHA	Shar311	PI 584435	<i>Ae. sharonensis</i>	Israel, Ashdod; 31°49'N, 34°40'E
SHA	Shar357	TA 2065	<i>Ae. sharonensis</i>	Israel, Palmahim II; 31°55'N, 34°42'E
SHA	Shar431	5 - 2	<i>Ae. sharonensis</i>	Israel, Palmahim I; 31°55'N, 34°42'E
SHA	Shar432	5 - 3	<i>Ae. sharonensis</i>	Israel, Palmahim I; 31°55'N, 34°42'E
SHA	Shar433	14661	<i>Ae. sharonensis</i>	Turkey, Elazig; 1.6 km NW of Elazig
SHA	Shar438	14666	<i>Ae. sharonensis</i>	Israel, near Cesarea, Sharon plain
SPE	Spel53	AE 378/80	<i>Ae. speltoides</i> ssp. <i>speltoides</i>	Israel, near Maagan Michael
SPE	Spel63	AE 404/82	<i>Ae. speltoides</i> ssp. <i>speltoides</i>	Israel, Ein Hamifratz, S of Akko
SPE	Spel66	AE 407/82	<i>Ae. speltoides</i> ssp. <i>ligustica</i>	Israel, NE of Giv'at Olga
SPE	Spel83	AE 522/78	<i>Ae. speltoides</i> ssp. <i>ligustica</i>	unknown
SPE	Spel102	AE 739/92	<i>Ae. speltoides</i> ssp. <i>speltoides</i>	Israel, 33 km sw Malatya
SPE	Spel103	AE 747/83	<i>Ae. speltoides</i> ssp. <i>speltoides</i>	Israel, Goilat, 17 km nw Beeszheba
SPE	Spel113	AE 921/87	<i>Ae. speltoides</i> ssp. <i>ligustica</i>	unknown
SPE	Spel136	PI 170203	<i>Ae. speltoides</i>	Turkey, 38 km SE K. Maras
SPE	Spel136	PI 487235	<i>Ae. speltoides</i>	Turkey, 39 km E Kahta
SPE	Spel141	PI 573448	<i>Ae. speltoides</i>	unknown
SPE	Spel151	PI 542274	<i>Ae. speltoides</i> ssp. <i>ligustica</i>	Iraq
SPE	Spel155	PI 560751	<i>Ae. speltoides</i>	Turkey, Kirkclareli; 41°20'N, 27°29'E
SPE	Spel173	TUR 02776	<i>Ae. speltoides</i>	Syria, Latakia; 35°40'N, 35°52'E
SPE	Spel179	TUR 02556	<i>Ae. speltoides</i>	Turkey, Cankiri; 40°31'N, 33°38'E
TAU	Tau469	TUR 02554	<i>Ae. speltoides</i> var. <i>speltoides</i>	Turkey, Adiyaman; 38°1'N, 38°31'E
TAU	Tau470	TUR 02564	<i>Ae. speltoides</i>	Turkey, Siirt; 37°38'N, 42°21'E
BOE	A663	PI 427529	<i>Ae. speltoides</i>	Turkey, Sanliurfa
BOE	A927	PI 427800	<i>Ae. speltoides</i>	Turkey, Sanliurfa
BOE	A949	PI 427822	<i>Ae. tauschii</i>	Turkey, Sanliurfa
BOE	A984	PI 427857	<i>T. booticum</i>	Turkey, Mardin/ 83.8 km west of Kiziltepe/ 670
BOE	A992	PI 427865	<i>T. booticum</i>	Iran, 34 km east of Kamiran/ 1900
			<i>T. booticum</i>	Iraq, 1 km northeast of Salahadin/ 1100
			<i>T. booticum</i>	Iraq, 21 km south of Harr/ 1000
			<i>T. booticum</i>	Iraq, 13 km west of Shaqlawa/ 1000

Symbol	Short name	Accession-No	Species	Origin	Source
BOE	A1129	PI 428007	<i>T. boeoticum</i>	Iraq, 21 km south of Hanit/ 1000	USDA
BOE	A1147	PI 503301	<i>T. boeoticum</i>	Turkey, Mardin/ 83.8 km west of Kiziltepe/ 670	USDA
BOE	A1231	PI 538597	<i>T. boeoticum</i>	Iraq, 13 km west of Shaqlawa/ 1000	USDA
BOE	A1256	PI 538623	<i>T. boeoticum</i>	Turkey, Bolu, 0 km east Mengen/ 700	USDA
URA	A388	787	<i>T. urartu</i>	Lebanon, G3246	USA/ KS
URA	A1122	PI 428000	<i>T. urartu</i>	Lebanon, between Kfarkouk and Aihha/	USDA
URA	A1127	PI 428005	<i>T. urartu</i>	Iraq, 7 km northeast of Shaqlawa/ 1000	USDA
URA	A1264	PI 554479	<i>T. urartu</i>	Turkey, Gaziantep, 19 km north of Gaziantep toward Yavuzeli/ 800	USDA
URA	A1399	PI 428187	<i>T. urartu</i>	Turkey, Mardin	USDA
URA	A1422	PI 428216	<i>T. urartu</i>	Turkey, Mardin	USDA
URA	A1463	PI 428271	<i>T. urartu</i>	Lebanon	USDA
URA	A1475	PI 428283	<i>T. urartu</i>	Lebanon	USDA
URA	A1484	PI 428294	<i>T. urartu</i>	Lebanon	USDA
URA	A1490	PI 428301	<i>T. urartu</i>	Lebanon	USDA
URA	A1528	PI 503319	<i>T. urartu</i>	Turkey, Mardin	USDA
URA	A1532	PI 538727	<i>T. urartu</i>	Turkey, Mardin	USDA
DIC	Dic-I	IG 110737	<i>T. turgidum ssp. dicoccoides</i>	Syria, Sweida, 2km north of Saleh, road to Busan	ICARDA
DIC	Dic-II	IG 45500	<i>T. turgidum ssp. dicoccoides</i>	Syria, Sweida, 40 km from Sweida between Sale and Malah	ICARDA
DIC	Dic-III	IP 560697	<i>T. turgidum ssp. dicoccoides</i>	Turkey, Siirt	USDA
ARA	Aral	1943	<i>T. araraticum</i>	Turkey, 45 km SE of Maras (Maras-Gaziantep)	Kyoto
ARA	AralI	1944	<i>T. araraticum</i>	Turkey, 45 km SE of Maras (Maras-Gaziantep)	Kyoto
ARA	AralII	1966	<i>T. araraticum</i>	Turkey, 45 km SE of Maras (Maras-Gaziantep)	Kyoto
ARA	AralIV	8451	<i>T. araraticum</i>	Iraq, 13.2 km S from Sulaymaniyah to Qara Dagh	Kyoto

Supplementary Table S5. Genes sequenced: references, chromosomal locations and functions

Locus	Symbol	Source	Chr	Function
acetyl-CoA-carboxylase	<i>ACCI</i>	Huang et al. 2002	2AS	Fatty acid biosynthesis
glucose-6-phosphate-dehydrogenase	<i>G6PDH</i>	Nemoto et al. 1999	Nm	PPC-pathway
glucose-6-phosphate/phosphate translocator	<i>GPT</i>	GenBank AF548741	Nm	Starch biosynthesis
3-phosphoglycerate kinase	<i>PGK1</i>	Huang et al. 2002	Nm	Calvin cycle
Q-Locus	<i>Q</i>	Faris et al. 2003	5AL	Domestication/free-threshing
TmAP1-gene	<i>Vrn1</i>	Yan et al. 2003	5AL	Vernalisation
NADH dehydrogenase	<i>ndhF</i>	Ogihara et al. 2002	cp	Electron transport

Locus No	locus number
Source	origin of sequences used
Chr	chromosome.
Nm	not mapped
Cp	chloroplast genome

Supplementary Table S6. Lines used for sequence analysis

D) Lines used for all loci:

ID No	Line	Access	Species	Origin	Source
Dic1	208	108-2	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Syria, 20 km NW of Suweida	Kyoto
Dic2	209	108-3	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Syria, 20 km NW of Suweida	Kyoto
Dic3	210	1921	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, 155 km W of Mardin	Kyoto
Dic4	211	1945	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, 45 km SE of Maras	Kyoto
Dic5	226	1991	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, 45 km SE of Maras	Kyoto
Dic6	233	8736B	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Iraq, SW of Rowanduz	Kyoto
Dic7	236	8805	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Iraq, N of Kursi, north slope of Jabal Sinjar	Kyoto
Dic8	239	8808	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Iraq, N of Kursi, north slope of Jabal Sinjar	Kyoto
Dic9	251	8915A	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, 17.3 km E from Silvan to Bitlis	Kyoto
Dic10	252	8915B	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, 17.3 km E from Silvan to Bitlis	Kyoto
Dic11	253	8935	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, 9.3 km SE from Ergani to Diyarbakir	Kyoto
Dic12	254	8937B	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, 9.3 km SE from Ergani to Diyarbakir	Kyoto
Dic13	256	8942	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Iran, 58.8 km N from Kermanshah to Ravansar	Kyoto
Dic14	257	8943	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Iran, 58.8 km N from Kermanshah to Ravansar	Kyoto
Dic15	260	14417	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Israel, Yehudiya	Kyoto
Dic16	261	14419	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Israel, Yehudiya	Kyoto
Dic17	263	14429	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Israel, Rosh Pina	Kyoto
Dic18	266	14451	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Israel, Bet Meir	Kyoto
Dic19	271	14476	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Israel, Tabigha	Kyoto
Dic20	272	14490	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Israel, Bat Shlomo	Kyoto
Dic21	274	14505	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Israel, Tayiba	Kyoto
Dic22	278	TUR 03396	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, Karacadag/ Diyarbakir	H. Özkan
Dic23	282	TUR 03371	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, Karacadag/ Diyarbakir	H. Özkan
Dic24	284	TUR 03402	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, Karacadag/ Diyarbakir	H. Özkan
Dic25	286	TUR 03399	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, Karacadag/ Diyarbakir	H. Özkan
Dic26	291	TUR 03558	<i>Triticum turgidum</i> ssp. <i>dicoccum</i>	Turkey, Sinop-Turkiye	H. Özkan
Dic27	293	TUR 03560	<i>Triticum turgidum</i> ssp. <i>dicoccum</i>	Turkey, Kastamonu-Turkiye	H. Özkan
Dic28	295	TUR 02456	<i>Triticum turgidum</i> ssp. <i>dicoccum</i>	Turkey, Sinop-Turkiye	H. Özkan
Dic29	296	TUR 02453	<i>Triticum turgidum</i> ssp. <i>dicoccum</i>	Turkey, Sinop-Turkiye	H. Özkan
Dic30	298	TUR 03565	<i>Triticum turgidum</i> ssp. <i>dicoccum</i>	Turkey, Kastamonu-Turkiye	H. Özkan
Dic31	214	1949	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, 45 km SE of Maras	Kyoto
Dic32	215	1951	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, 45 km SE of Maras	Kyoto

Dic33	224	1976B	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, 45 km SE of Maras	Kyoto
Dic34	231	8541	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Iraq, 20.3 km S from Sulaymaniyah to Qara	Kyoto
Dic35	232	8736A	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Iraq, SW of Rowanduz	Kyoto
Dic36	237	8806	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Iraq, N of Kursi, north slope of Jabal Sinjar	Kyoto
Dic37	245	8815	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Iraq, N of Kursi, north slope of Jabal Sinjar	Kyoto
Dic38	276	14517	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Israel, Kochav Hashahar	Kyoto
Dic39	280	TUR 03358	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Turkey, Karacadag, Diyarbakir	H. Özkan
Tdu/A18		Dic177	<i>Triticum turgidum</i> ssp. <i>durum</i>	Italy, Cultivar 1990, Ofanto	Italy
ARA-001	TR1	PI352264	<i>Triticum araraticum</i> Jakubz.	Armenia; 40°30'N, 45°0'E	USDA
ARA-038	TR38	1902	<i>Triticum araraticum</i> Jakubz.	Armenia; 8 km W of Garni	Kyoto
ARA-044	TR44	1966	<i>Triticum araraticum</i> Jakubz.	Turkey, 45 km SE of Maras (Maras-Gaziantep)	Kyoto
ARA-046	TR46	8452	<i>Triticum araraticum</i> Jakubz.	Iraq, 13.2 km S from Sulaymaniyah to Qara Dagh	Kyoto
ARA-100	TR100	8944	<i>Triticum araraticum</i> Jakubz.	Iran, 12.2 km NW from Karand to Qasri Shirin	Kyoto
TIM-102	TR102	107-4	<i>Triticum timopheevii</i> ssp. <i>typicum</i>	Kyoto	Kyoto
TIM-103	TR103	107-5	<i>Triticum timopheevii</i> ssp. <i>typicum</i>	Kyoto	Kyoto
TIM-106	TR106	1820	<i>Triticum timopheevii</i> ssp. <i>viticulosum</i>	USSR	Kyoto
TIM-108	TR108	TRI4349/94	<i>Triticum timopheevii</i> var. <i>timopheevii</i>	Hungary	IPK
TIM-109	TR109	TRI5351/74	<i>Triticum timopheevii</i> var. <i>timopheevii</i>	Georgia	IPK
TIM-111	TR111	TRI772/79	<i>Triticum timopheevii</i> var. <i>timopheevii</i>	Ethiopia	IPK
A1Spe	A-346	PI 542256	<i>Aegilops speltoides</i> var. <i>ligistica</i>	Turkey, Adiyaman; 37°58'N, 38°37'E	USDA
A2Spe	A-349	PI 542269	<i>Aegilops speltoides</i> var. <i>speltoides</i>	Turkey, Gaziantep; 37°5'N, 37°24'E	USDA
A3Spe	A-351	PI 542274	<i>Aegilops speltoides</i> var. <i>speltoides</i>	Turkey, Adiyaman; 38°01'N, 38°31'E	USDA
A4Spe	A-352	PI 560530	<i>Aegilops speltoides</i> var. <i>speltoides</i>	Turkey, Siirt; 38°04'N, 41°47'E	USDA
A5Spe	A-353	PI 560531	<i>Aegilops speltoides</i> var. <i>speltoides</i>	Turkey, Siirt; 37°45'N, 42°10'E	USDA
A7Sea	Ae-185	PI 599130	<i>Aegilops searsii</i>	Jordan, Tumeira; 32°23'N, 35°59'E	USDA
A8Sea	Ae-186	PI 599131	<i>Aegilops searsii</i>	Jordan, El Buweida; 32°21'N, 36°2'E	USDA
A9Bic	Ae-447	3-3	<i>Aegilops bicornis</i>	Egypt, 21 km W of Alexandria	KYOTO
A10Bic	Ae-448	5782	<i>Aegilops bicornis</i>	Egypt, Matruh	USDA
A11Lon	Ae-153	PI 604120	<i>Aegilops longissima</i>	Israel, Beit-Lid; 32°19'N, 34°54'E	KYOTO
A12Lon	Ae-172	PI 604141	<i>Aegilops longissima</i>	Israel, Rehovot; 31°51'N, 34°48'E	USDA
A13Sha	Ae-307	PI 584431	<i>Aegilops sharonensis</i>	Israel, Palmahim I; 31°55'N, 34°42'E	USDA
A14Sha	Ae-294	PI 584418	<i>Aegilops sharonensis</i>	Israel, Palmahim I; 31°55'N, 34°42'E	USDA
A15Spe	Ae-335	PI 487233	<i>Aegilops speltoides</i> var. <i>speltoides</i>	Syria, Aleppo; 37°0'N, 36°41'E	USDA
A16Spe	Ae-333	PI 487231	<i>Aegilops speltoides</i> var. <i>speltoides</i>	Syria, Aleppo; 36°10'N, 36°50'E	USDA
A17Tau	Afghan 27 TQ 57		<i>Aegilops tauschii</i>	Afghanistan	T. Miller

II) additional diploid AA lines used per locus:

ID No	Line	Access	Species	Origin	Source	Einkorn-Haplotypes
ACCI						
Tm209	ID 209	BGRC 20451	<i>Triticum monococcum</i>	Balkan	BGRC	I
Tm226	ID 226	BGRC 36546	<i>Triticum monococcum</i>	Balkan	BGRC	VIII
Tb604	ID 604	PI 427470	<i>Triticum boeoticum</i>	Turkey, Mardin, Kiziltepe	USDA	III
Tb746	ID 746	PI 427614	<i>Triticum boeoticum</i>	Turkey, Urfa	USDA	IV
Tb1108	ID 1108	PI 427985	<i>Triticum boeoticum</i>	Turkey, Cankiri, Cerkes	USDA	VI
Tb1272	ID 1272	PI 554488	<i>Triticum boeoticum</i>	Turkey, Urfa, Siverek	USDA	II
Tb1292	ID 1292	PI 554525	<i>Triticum boeoticum</i>	Turkey, Bursa, Yenisehir	USDA	VII
Tml331	ID 1331	MG 4278	<i>Triticum monococcum</i>	Italy	USDA	V
Tul447	ID 1447	PI 428249	<i>Triticum urartu</i>	Turkey, Urfa	USDA	X
Tu1556	ID 1556	PI 538750	<i>Triticum urartu</i>	Lebanon	USDA	IX
G6PDH						
Tm04	ID 04	PI 94740	<i>Triticum monococcum</i>	Spain	Can/A	I
Tb226	ID 226	BGRC 36546	<i>Triticum monococcum</i>	Balkan	BGRC	IV
Tu388	ID 388	787	<i>Triticum urartu</i>	Lebanon, G 3246	USA/KS	V
Tb754	ID 754	PI 427622	<i>Triticum boeoticum</i>	Turkey, Diyarbakir	USDA	III
Tb875	ID 875	PI 427747	<i>Triticum boeoticum</i>	Iraq, Zawita, Suara Tuka	USDA	II
GPT						
Tm04	ID 04	PI 94740	<i>Triticum monococcum</i>	Spain	Can/A	I
Tu393	ID 393	831	<i>Triticum urartu</i>	Iran, Bakhtaran, G 3221	USA/KS	II
Tbl1308	ID 1308	PI 554547	<i>Triticum boeoticum</i>	Turkey, Konya, Beysehir	USDA	IV
Tul1404	ID 1404	PI 428192	<i>Triticum urartu</i>	Turkey, Mardin	USDA	III
PGK1						
Tml5	ID 15	PI 264935	<i>Triticum monococcum</i>	Greece, Crete	Can/A	V
Tu393	ID 393	831	<i>Triticum urartu</i>	Iran, Bakhtaran, G 3221	USA/KS	VIII
Tb585	ID 585	PI 427445	<i>Triticum boeoticum</i>	Turkey, Tekirdag	USDA	I
Tb600	ID 600	PI 427463	<i>Triticum boeoticum</i>	UDSSR, Azerbaijan	USDA	VII
Tb751	ID 751	PI 427619	<i>Triticum boeoticum</i>	Turkey, Urfa, Siverek	USDA	VI
Tb766	ID 766	PI 427635	<i>Triticum boeoticum</i>	Turkey, Urfa, Siverek	USDA	II

Tb1141	ID 1141	PI 470718	<i>Triticum boeoticum</i>	Turkey, Nevsehir, Urgup	USDA	III
Tb1258	ID 1258	PI 538625	<i>Triticum boeoticum</i>	Turkey, Denizli	USDA	IV
Tu1455	ID 1455	PI 428263	<i>Triticum urartu</i>	Lebanon	USDA	IX
<i>Q</i>						
Tm04	ID 04	PI 94740	<i>Triticum monococcum</i>	Spain	Can/A	I
Tb386	ID 386	747	<i>Triticum boeoticum</i>	Turkey, G 1878	USA/KS	V
Tb585	ID 585	PI 427445	<i>Triticum boeoticum</i>	Turkey, Tekirdag	USDA	VII
Tb597	ID 597	PI 427458	<i>Triticum boeoticum</i>	Turkey, Kirsehir	USDA	VII
Tb754	ID 754	PI 427622	<i>Triticum boeoticum</i>	Turkey, Diyarbakir	USDA	III
Tb862	ID 862	PI 427733	<i>Triticum boeoticum</i>	Iraq, Dohuk	USDA	VI
Tb870	ID 870	PI 427741	<i>Triticum boeoticum</i>	Iraq, Suwa Tuka	USDA	IV
Tm1259	ID 1259	PI 538721	<i>Triticum monococcum</i>	Turkey, Canakkale, Ecebat	USDA	II
Tb1290	ID 1290	PI 554522	<i>Triticum boeoticum</i>	Turkey, Izmir	USDA	IX
Tu1404	ID 1404	PI 428192	<i>Triticum urartu</i>	Turkey, Mardin	USDA	X
Tu1425	ID 1425	PI 428224	<i>Triticum urartu</i>	Turkey, Mardin	USDA	XII
Tu1447	ID 1447	PI 428249	<i>Triticum urartu</i>	Turkey, Urfa	USDA	XII
Tu1504	ID 1504	PI 428317	<i>Triticum urartu</i>	Iran, Bakhtaran	USDA	XI
Tu1547	ID 1547	PI 538742	<i>Triticum urartu</i>	Lebanon	USDA	XIVb
<i>VRNI</i>						
Tb226	ID 226	BGRC 36546	<i>Triticum monococcum</i>	Balkan	BGRC	III
Tu388	ID 388	787	<i>Triticum urartu</i>	Lebanon, G 3246	USA/KS	VIII
Tb682	ID 682	PI 427548	<i>Triticum boeoticum</i>	Turkey, Mardin, Nusaybin	USDA	V
Tb751	ID 751	PI 427619	<i>Triticum boeoticum</i>	Turkey, Urfa, Siverek	USDA	VI
Tb752	ID 752	PI 427620	<i>Triticum boeoticum</i>	Turkey, Urfa, Siverek	USDA	I
Tb760	ID 760	PI 427629	<i>Triticum boeoticum</i>	Turkey, Urfa, Siverek	USDA	VII
Tb1002	ID 1002	PI 427875	<i>Triticum boeoticum</i>	Iraq, Shaqlawa	USDA	IV
Tb1252	ID 1252	PI 538619	<i>Triticum boeoticum</i>	Turkey, Yozgat, Sorgun	USDA	II
<i>ndhF</i>						
Tm04	ID 04	PI 94740	<i>Triticum monococcum</i>	Spain	Can/A	I
Tu388	ID 388	787	<i>Triticum urartu</i>	Lebanon, G 3246	USA/KS	II

III) additional tetraploid AAGG and hexaploid AABBDD lines used:

<i>ACCI</i>					
ARA-054	TR54	8597	<i>Triticum araraticum</i> Jakubz.	Iraq, 52.4 km SW from Sulaymaniyah to Surdash	Kyoto
TIM-104	TR104	1818 (only used for genome G sequence)	<i>Triticum timopheevii</i> ssp. <i>typicum</i>	USSR	Kyoto
<hr/>					
<i>ndhF</i>					
ARA-054	TR54	8597	<i>Triticum araraticum</i> Jakubz.	Iraq, 52.4 km SW from Sulaymaniyah to Surdash	Kyoto
ARA-066	TR66	8706	<i>Triticum araraticum</i> Jakubz.	Iraq, 11.4 km NE from Koi Sanjaq to Ranya	Kyoto
ARA-092	TR92	8908	<i>Triticum araraticum</i> Jakubz.	Turkey, 26.3 km NE from Mardin to Midyat	Kyoto
ARA-098	TR98	8938	<i>Triticum araraticum</i> Jakubz.	Turkey, 39.9 km N from Elazig to Hozat	Kyoto
TIM-104	TR104	1818	<i>Triticum timopheevii</i> ssp. <i>typicum</i>	USSR	Kyoto
TIM-105	TR105	1819	<i>Triticum timopheevii</i> ssp. <i>typicum</i>	USSR	Kyoto
TIM-107	TR107	1821	<i>Triticum timopheevii</i> ssp. <i>viticulosum</i>	USSR	Kyoto
TIM-110	TR110	TRI5352/75	<i>Triticum timopheevii</i> ssp. <i>timopheevii</i>	USSR, Caucasus	IPK
AES01			<i>Triticum aestivum</i>	Italy, Cultivar Sagittario	Italy
AES02			<i>Triticum aestivum</i>	Italy, Cultivar Mieti	Italy
AES03			<i>Triticum aestivum</i>	Italy, Cultivar Bilancia	Italy
AES04			<i>Triticum aestivum</i>	Italy, Cultivar Eureka	Italy

Supplementary Table S7. Publicly available lines of known sequences

Locus	Short name	Access-Nos	Species	Genome
<i>ACCI</i>	Tb343502	AF343502	<i>T. boeoticum</i>	A ^m
	Tb343504	AF343504	<i>T. boeoticum</i>	A ^m
	Tm343513	AF343513	<i>T. monococcum</i>	A ^m
	Tm343515	AF343515	<i>T. monococcum</i>	A ^m
	Tm343517	AF343517	<i>T. monococcum</i>	A ^m
	Tu343518	AF343518	<i>T. urartu</i>	A ^u
	Tdi343511A	AF343511	<i>T. dicoccoides</i>	A
	Tdi343499A	AF343499	<i>T. dicoccoides</i>	A
	Tdi343512A	AF343512	<i>T. dicoccoides</i>	A
	Tti343497A	AF343497	<i>T. timophevii</i>	A
	Tti343514A	AF343514	<i>T. timophevii</i>	A
	Tae029897A	AF029897	<i>T. aestivum</i>	A
	Tdi343500B	AF343500	<i>T. dicoccoides</i>	B
	Tdi343506B	AF343506	<i>T. dicoccoides</i>	B
	Tdi343507B	AF343507	<i>T. dicoccoides</i>	B
	Tae343510B	AF343510	<i>T. aestivum</i>	B
	Tti343503G	AF343503	<i>T. timophevii</i>	G
	Tti343505G	AF343505	<i>T. timophevii</i>	G
	Tae029896D	AF029896	<i>T. aestivum</i>	D
	Tae343498D	AF343498	<i>T. aestivum</i>	D
	Sea343522	AF343522	<i>Ae. searsii</i>	S
	Sea343524	AF343524	<i>Ae. searsii</i>	S
	Sea343528	AF343528	<i>Ae. searsii</i>	S
	Sea343529	AF343529	<i>Ae. searsii</i>	S
	Bic343521	AF343521	<i>Ae. bicornis</i>	S
	Lon343532	AF343532	<i>Ae. longissima</i>	S
	Lon343531	AF343531	<i>Ae. longissima</i>	S
	Sha343526	AF343526	<i>Ae. sharonensis</i>	S
	Sha343525	AF343525	<i>Ae. sharonensis</i>	S
<i>G6PDH</i>	Spe343520	AF343520	<i>Ae. speltoides</i> ssp. <i>speltoides</i>	S
	Spe343523	AF343523	<i>Ae. speltoides</i> ssp. <i>ligistica</i>	S
	Spe343536	AF343536	<i>Ae. speltoides</i> ssp. <i>ligistica</i>	S
	Spe343527	AF343527	<i>Ae. speltoides</i> ssp. <i>speltoides</i>	S
	Spe343530	AF343530	<i>Ae. speltoides</i> ssp. <i>speltoides</i>	S
	Spe343533	AF343533	<i>Ae. speltoides</i> ssp. <i>speltoides</i>	S
	Spe343534	AF343534	<i>Ae. speltoides</i> ssp. <i>speltoides</i>	S
	Spe343535	AF343535	<i>Ae. speltoides</i> ssp. <i>ligistica</i>	S
	Tae029455	AB029455	<i>T. aestivum</i>	A
	Tae029456	AB029456	<i>T. aestivum</i>	A
	Tae011441	AB011441	<i>T. aestivum</i>	A
	Tae029454	AB029454	<i>T. aestivum</i>	A
<i>GPT</i>	Tae548741	AF548741	<i>T. aestivum</i>	A
<i>PGK1</i>	Tu343474A	AF343474	<i>T. urartu</i>	A ^u
	Tdi343481A	AF343481	<i>T. dicoccoides</i>	A
	Tti343477A	AF343477	<i>T. timophevii</i>	A
	Tae343475A	AF343475	<i>T. aestivum</i>	A
	Tdi343476B	AF343476	<i>T. dicoccoides</i>	B

Note: These AES lines are not included in the analyses. They were used to design the primer.

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Tae343480B	AF343480	<i>T. aestivum</i>	B
Tae343478D	AF343478	<i>T. aestivum</i>	D
Spe343483	AF343483	<i>Ae. speltoides ssp. speltoides</i>	S
Spe343482	AF343482	<i>Ae. speltoides ssp. ligistica</i>	S
Tau343479D	AF343479	<i>Ae. tauschii</i>	D
<hr/>			
<i>Q</i>	Tm170867	<i>T. monococcum</i>	A ^m
Tu702958	AY702958	<i>T. urartu</i>	A ^u
Ttu702955	AY702955	<i>T. turgidum</i>	A
Tdic702957	AY702957	<i>T. dicoccoides</i>	A
Tdic714343	AY714343	<i>T. dicoccum</i>	A
Ttu702959	AY702959	<i>T. turgidum carthlicum</i>	A
Ttu714339	AY714339	<i>T. turgidum polonicum</i>	A
Tae702960	AY702960	<i>T. aestivum spelta</i>	A
Tae714342	AY714342	<i>T. aestivum macha</i>	A
Tae714340	AY714340	<i>T. aestivum spelta</i>	A
Tae714341	AY714341	<i>T. aestivum spelta</i>	A
Tae702956	AY702956	<i>T. aestivum</i>	A
<hr/>			
<i>VRN1</i>	Tm244508a	<i>T. monococcum</i>	A ^m
Tm244508b	AY244508	<i>T. monococcum</i>	A ^m
Tm244509a	AY244509	<i>T. monococcum</i>	A ^m
Tm244509b	AY244509	<i>T. monococcum</i>	A ^m
Tdu466448A	AY466448	<i>T. durum</i>	A
Tdu466447B	AY466447	<i>T. durum</i>	B
Atau466446	AY466446	<i>Ae. tauschii</i>	D

Access-Nos: published Accession-Numbers
 Genome: published Genome
 Short name: name in our dataset

Supplementary Table S8. Primers used for gene amplification and sequencing

Locus	Primer-name	Primer-sequence	Supplier
ACC1	AA10-1132FOR	ACT GAC CGG ACC TTG ATT TTC	OPERON
	AA11-1153REV	AGA AAA TCA AGG TCC GGT CAG	OPERON
	AA12-1144REV	AGG TCC GGT CAG TTT ACA AAT C	OPERON
	AB06-168FOR	CGC CTG TAA GCT TCA TAT GTT ATT C	SIGMA
	AB07-1309REV	AAG CCC AAA TGG AAA AAC TAG C	SIGMA
	AB08-657FOR	CTT TTG AAC ATT CCT CTG GAC TTA A	SIGMA
	AB09-1320REV	ATA CTT GGT CAA AGC CCA AAT G	SIGMA
	Ac17-FOR4	AGG TTG AGC ATC CAG TCA CC	OPERON
	AcZ3-REV	GTT ATT GCT GCT CTA GAC ACT C	OPERON
	AG01-193FOR	CTT GCA GGC TAG AAA TGT ATG C	SIGMA
	AG02-1509REV	CCA TAT GCA AAA ACA TGT CCT G	SIGMA
	Ti02-1304R	AAA ACG CAG CCC AAT TTT C	OPERON
	Ti03-169F	CCT GGA AGC TTC GTA TGT TAT TC	OPERON
	Ti04-1336R	GTC AAA GCC CAA ATG GAA AAG	OPERON
G6PDH	G601-1297FOR	GCA GGG AAG AAA TGA GTT TGT C	SIGMA
	G602-1695REV	GTG GGT GGT ATC CAG ATG TAA C	SIGMA
	G623-268FOR	GTT TAC GCG ATT TTG TGC AG	OPERON
	G628-626REV	CAG TCT CAG TGA CAG AAT G	OPERON
GPT	GT08-298FOR	CCA ATC AAC GGT CTA AAT CAG C	SIGMA
	GT14-891REV	ATA CAG GCA TCG GAA ATG ACT C	SIGMA
	GT26-57FOR	CAA ATT GCC TCC TGC TC	OPERON
	GT27-54FOR	AAA CAA ATT GCC TCC TGC TC	OPERON
PGK1	PK11-FOR1	TCG TCC TAA GGG TGT TAC TCC TAA	OPERON
	PK19-REV	AGG GAT TCG ATA ACC CCA ATC	OPERON
	PT01-44FOR	GTG CCA CGA TTA TCT GAG CTT C	SIGMA
	PT05-211FOR	AGT TGA AAA ATT GGT GGC TGA C	SIGMA
	PT11-1063REV	GGA CGG TCT ACA GAA AAA TTC C	SIGMA
	PU02-1064REV	GGG ACG GTC TAC AGA AAA ATT G	SIGMA
	PU03-49FOR	CCG ATT ATC CGA GCT TCT TG	SIGMA
	PU09-216FOR	AGA AAT TGG TGG CTG ACC TG	OPERON
Q	Q05-748FOR	CGA CAT CAA CTT CAA TCT GAG C	SIGMA
	Q08-975REV	TCA ACT TCG CTG TCA AAG AGG	SIGMA
	QA01-55F	ATC CAA GCC TAG TTG ATT GCT G	OPERON
	QA05-856R	TGA TGA TAA TGT GGG TAT CAG G	OPERON
	QB03-39F	TGA AGC AGG TAA TCA TCT AAG CTA C	OPERON
	QB04-34F	GGA TTT GAA GCA GGT AAT CAT C	OPERON
	QB05-863R	GCG ATG ATA ATG TGG ATA TCA GG	OPERON
VRN1	A1F-VA1-F ¹	TCA GAT TCT AGA CTG AGA TGT TCA A	SIGMA
	A1R-VA1-R ¹	GAT GTG GCT CAC CAT CCA CG	SIGMA
	B1F-VB1/VD1F	TCA GAT TCT AGA CTG AGA TAT TCA C	SIGMA
	B1R-VB1R	GAT GTG GCT AAC CAT CCA CA	SIGMA
	AE01-22FOR	TAT AGG AAA CTG AAG GCG AAG G	SIGMA
	AE11-640REV	GCA GCA AGA ACG ATG TAA TGA G	SIGMA
ndhF	nd01-1438FOR	GGA AAA AGG ATA CCC AAA GGA G	SIGMA
	nd02-2156REV	ATT CGA CCT CCC CCT ACA TAT T	SIGMA

Note: Cloned PCR products were sequenced using standard sequencing primers:

¹ Sherman et al. 2004

unil CGTTGTAAAACGACGCCAGT

revl CAGGAAACAGCTATGACCATG

Supplementary Table S9. Overview of the loci, their amplification conditions, fragment length, origin and chromosomal position for haplotype analyses

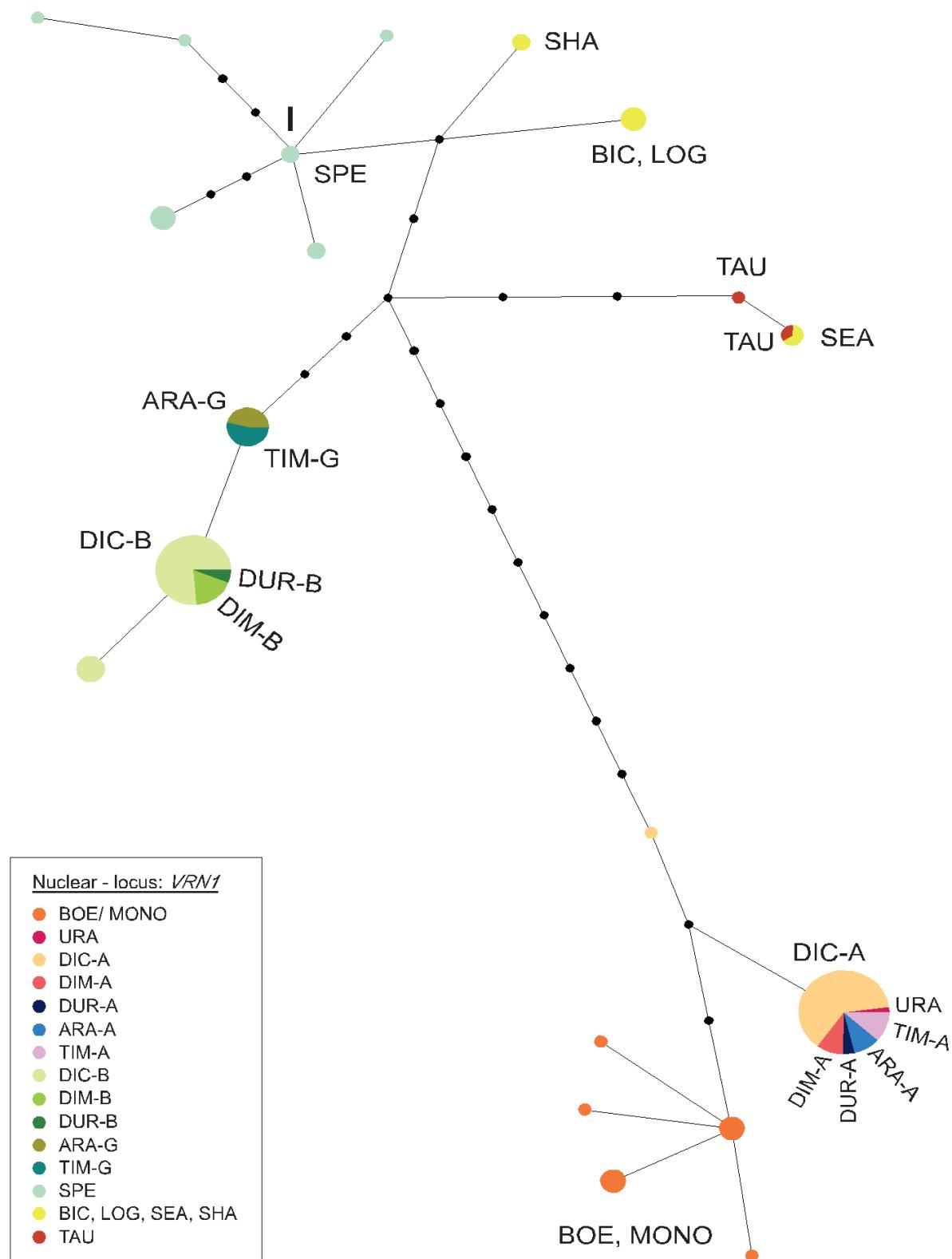
Gene	Species	Amplicon Genome	PCR-Primer	DNASP				PCR conditions			
				Total in bp	Frag in bp	Com sites	Seq-Primer	Length in bp	Anaef Temp	Anaef Time	Elong Time
<i>ACCI</i>	BOE/ MONO/ URA	A	Ac17-AcZ3	810	1375	366	Ac17, AcZ3	810	63.0	40	50
	DIC/ DU/ARA/TIM	A+B/G**	Ac17-AcZ3	810			Ac17, AcZ3	810	63.0	40	28
	A+B**/G	AG01-AG02		1317				63.0	40	85	31
	DIC/DU/ARA/TIM	A					AA11	960			
	ARA/TIM	A					AA10	380			
	ARA/TIM	A					AA12	951			
	DIC/DU	B	AB06-AB07	1150			AB06, AB07	1150	63.5	40	75
	ARA/TIM	G	AB06-AB07	1150			AB06, AB07	1150	54.5	20	75
							AB08	652			
							Ti02	1110			
							AB08-AB09	664	63.5	30	50
							Ti03, Ti04	1168	59.0	30	31
							E1, AG02	1365	62.0	40	75
							E3	799			
							E4	677			
							Ac17-AcZ3	810	63.0	40	55
											28
<i>G6PDH</i>	BOE/ MONO/ URA	A	G601-G602	749	764	537	G601, G602	62.5	40	50	29
	DIC/ DU/	A+B**	G601-G602	749				62.5	40	50	29
	A		diff								
	B		G601-G602				-				
							G623	500			
							G628	550			
	ARA/TIM	A+G***	G601-G602	749				62.5	40	50	29
	BIC/ LOG/ SEA/	S*	G601-G602	749			G601, G602	62.5	40	50	29
	SHA/ SPE										
<i>GPT</i>	BOE/ MONO/ URA	A	GT08-GT14	674	673		GT08, GT14	674	63.5	40	50
	DIC/ DU/ARA/TIM	A+B/G**	GT08-GT14	674			GT08, GT14	674	63.5	40	29
	DIC/ DU/ARA/TIM	A	diff								
	DIC/ DU/ARA/TIM	B/G	GT08-GT14				GT26	650			
							GT27	650			

BIC/ LOG/ SEA/ SHA/ SPE	S	GT08-GT14	674	GT08, GT14	674	63.5	40	50	29
<i>PGK1</i>	BOE/ MONO/ URA A DIC/ DU/ARA/TIM A	PK11-PK19 PU03-PU02	715 1016	1169 665	PK11, PK19 PU03, PU02	715 1016	61.0 63.5	40 40	28 29
	B/G	PT01-PT11	1020		PT01, PT11 PT05	1020 850	63.5 EA01, EA02	40 1107	70 60.5
BIC/ LOG/ SEA/ SHA/ SPE	S*	EA01-EA02	1107		PT13 PK19	752 717	752 61.0	75 40	29 50
		PK11-PK19	715		PK11, PK19	715	61.0	40	29
<i>Q</i>	BOE/ MONO/ URA A DIC/ DU/ARA/TIM A+B**/G	Q05-Q08 Q05-Q08	919 919	988 917	Q05, Q08 Q05, Q08	919 919	64.0 63.0	40 30	29 50
	A	Q05-Q08	919		QA01	860			33
	B/G	Q05-Q08	919		QB03	880			
<i>ARA/TIM</i>	A	QA01-QA05	802		QA01, QA05	802	61.0	30	29
<i>ARA/TIM</i>	G	QB04-QB05	830		QB04, QB05	830	61.0	30	29
BIC/ LOG/ SEA/ SHA/ SPE	S*	Q05-Q08	919		Q05, Q08	919	63.0	30	33
<i>Vrn1</i>	BOE/ MONO/ URA A DIC/ DU/ARA/TIM A	AE01-AE11 A1F-A1R	620 816	1155 816	304 AE01, AE11 A1F, A1R	620 816	63.0 65.0	40 40	29 55
	B/G	B1F-B1R	816		B1F, B1R	816	60.0	40	29
BIC/ LOG/ SEA/ SHA/ SPE	S*	B1F-B1R	816		B1F, B1R	816	60.0	40	29
<i>ndhF</i>	BOE/ MONO/ URA cp DIC/ DU/ARA/TIM cp	nd01-nd02 nd01-nd02	719 719	719 719	nd01, nd02 nd01, nd02	719 719	63.0 63.0	40 40	29 50
BIC/ LOG/ SEA/ SHA/ SPE	cp	nd01-nd02	719		nd01, nd02	719	63.0	40	29
						6843 bp	4181 bp		
Anneal Temp	Anaeling temperature								
Anneal Time	Anaeling time								
Chr:	Chromosome on which the gene is located								
Com sites:	Part of the total alignment (including gaps), present for ALL lines								
Cp:	Chloroplast genome								
Diff:	sequence-difference								

Elong. Time	Elongation time
Frag in bp:	Amplified fragment per species
Length in bp:	Length of the amplified fragment
Seq-Primer:	Sequencing primer
Sequence-Source:	Published and unpublished sources of sequences used for primer design. BOE etc. see Figure legend for Fig. 2
Species:	
Symbol:	Gene symbol
Total in bp:	Total alignment-length (without A6 and Barley)
*	Cloning used for heterozygotes lines
**	Cloning used for verification
***	Cloning used, because no genome specific primer-combination available yet
„*-Position“	all genomes standing before this star

Supplementary Table 10. Genbank numbers of the deposited gene sequences

<i>ACCI</i>	DQ290259-DQ290360; DQ290363-DQ290375; DQ364823-DQ364846
<i>G6PDH</i>	DQ290378-DQ290475; DQ290478-DQ290489; DQ364847-DQ364868
<i>GPT</i>	DQ290492-DQ290581; DQ290583-DQ290593; DQ364869-DQ364890
<i>PGK1</i>	DQ290658-DQ290757; DQ290760-DQ290771; DQ364891-DQ364912
<i>Q</i>	DQ290774-DQ290827; DQ290834-DQ290888; DQ290891-DQ290904; DQ364913-DQ364934
<i>rRNAI</i>	DQ291016-DQ291112; DQ291115-DQ291125; DQ364935-DQ364956
<i>ndhF</i>	DQ290596-DQ290642; DQ290644-DQ290655; DQ304659; DQ304661-DQ304678; DQ660429-DQ660432

MJ network for *VRN1***Fig. S1** - MJ network for *VRN1* haplotypes (82 lines, 137 sequences).

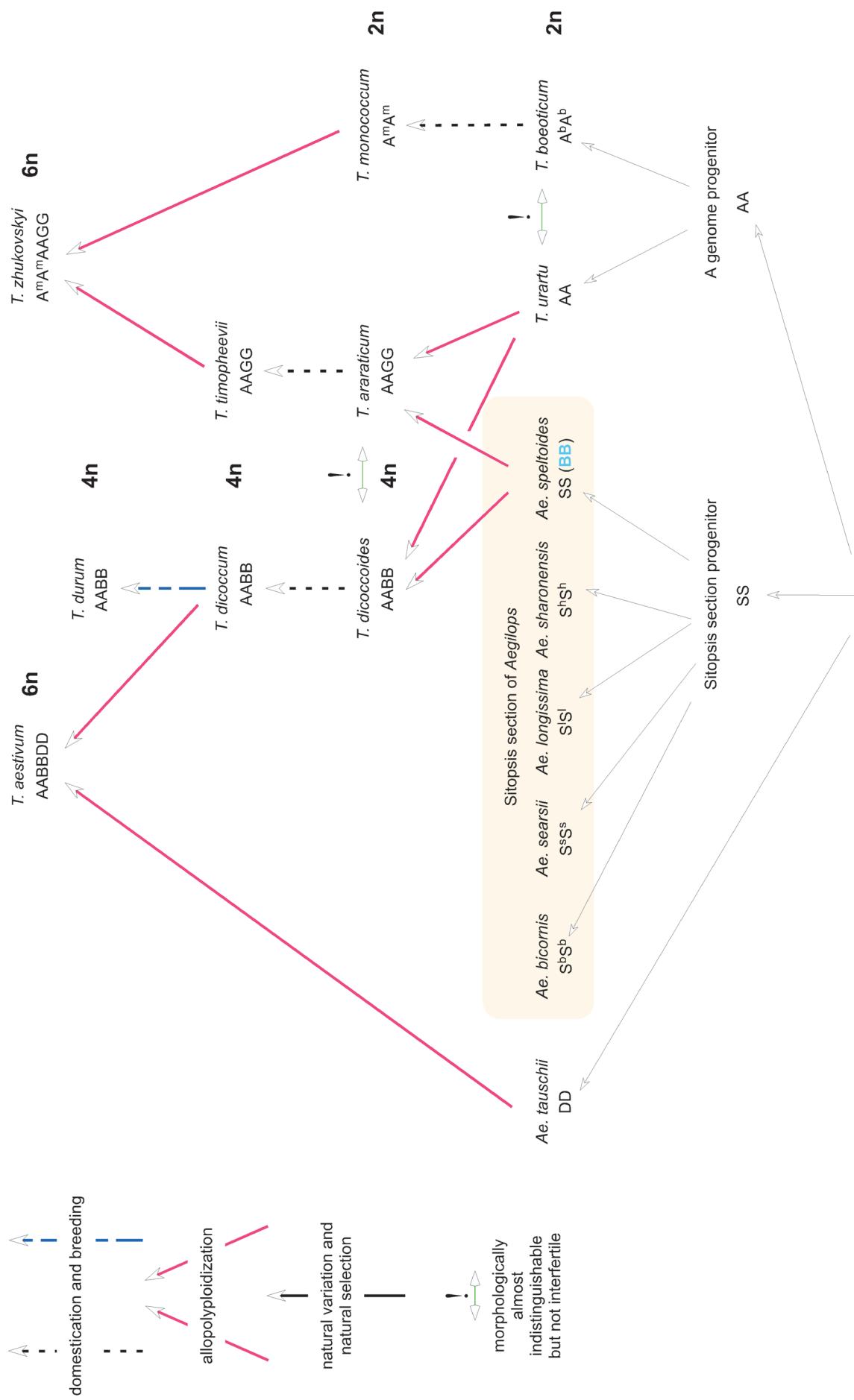


Fig. S2 - Overview of wheat evolution and events. *Aegilops* and *Triticum* nomenclature based on van Slageren (1994) and Dorofeev et al. (1979).

Chapter 5

Geography and domestication of wild emmer wheat (*T. dicoccoides*)

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Abstract

One of the first cereals domesticated by humans in the Fertile Crescent was the wild tetraploid emmer wheat (*T. dicoccoides*) about 11,000 years ago. This step provided the key for subsequent bread wheat evolution. Wild emmer was first discovered in 1906 in eastern Galilee on the slopes of Mount Hermon by Aaron Aaronsohn. His studies of geographical distribution and ecological requirements greatly contributed to our understanding of wheat domestication. In this minireview, we summarize several issues concerning the geography of wild emmer wheat and the investigations on the place of emmer domestication.

The nomenclature in this paper follows Dorofeev et al. (1979) and Zohary and Hopf (2000), and indicates with *T. dicoccoides* wild emmer *Triticum dicoccoides* (Körn. ex Aschers. & Graebn.) Schweinf., with *T. dicoccum* (*T. dicoccon*) domesticated emmer *Triticum dicoccum* (Schrank) Schübler, with *T. durum* the domesticated free-threshing hard or durum wheat *Triticum durum* Desf. and with *T. aestivum* the bread wheat *Triticum aestivum* L.

Wheat is one of the most important crops in the world and the stable food in more than 40 countries where it is the basis for over 35% of the global population (Williams 1993). It provides more than 60-65% of calories and protein for human nutrition together with rice and maize (Gill et al. 2004). Modern wheat cultivars belong primarily to two groups: I) tetraploid wheats, like *Triticum dicoccoides* (2n=28, AABB) and II) hexaploid bread wheat, *T. aestivum* (2n=42, ABBDD).

Wild emmer wheat (2n=4x=28; genome AABB) was first time recognized by Körnicke, a German scientist, in 1873 in the herbarium of the National Museum of Vienna among stems of wild barley that were collected by the botanist Kotschy in 1855 in Rasheyya on the northwestern slope of Mount Hermon, southern Lebanon (Feldman and Millet 2001). On June 18, 1906, wild emmer wheat was discovered in the field by Aaron Aaronsohn, an agronomist from Israel, in a vineyard at Rosh Pinna, Eastern Galilee, Israel (Feldman and Millet 2001). He recognized that wild emmer is the progenitor of cultivated wheats and suggested to use wild emmer as a source to improve bread wheat. The re-discovery of wild emmer by Aaronsohn in 1906 and his studies of its geographical distribution and ecological requirements greatly contributed to our understanding of wheat domestication and wheat improvement.

Wild emmer is an annual, predominantly self-pollinated, tetraploid wheat with large and brittle ears and elongated grains similar to domesticated emmer and durum wheat. Wild emmer hybridizes with domesticated tetraploid wheats, and the hybrids are fertile. The species has brittle ears that disarticulate at maturity into individual spikelets bearing relatively large seeds. Previous studies have shown that wild emmer exhibits a wide range of variation in morphological and genetical characters and two main races were recognized (Harlan and Zohary 1966; Mori et al. 2003; Ozkan et al. 2005; Luo et al. 2007). These are a western Palestine race and a eastern Turkish-Iraqi race. The two races are geographically separated (fig. 1) and morphologically distinct. Sachs (1953), working with a single representative from each race, showed that they were also cytogenetically distinct. Morphological variation within the Turkish-Iraqi race led him to suggest that this race may also show variation in chromosome differentiation. Important unique chromosomal translocations were also found in wild emmer populations, particularly in the Turkish-Iraqi race (Kawahara et al. 1993; Nishikawa et al. 1994; Joppa et al. 1995; Kawahara and Nevo et al. 1996).

The geographical distribution of wild emmer wheat reported by Harlan and Zohary (1966), Johnson (1975), Zohary and Hopf (2000) and Ozkan et al. (unpublished), includes the western Fertile Crescent, the central part of southeastern Turkey and areas in eastern Iraq and western Iran (fig. 1). The center of

variability is thought in the Jordan valley (Harlan and Zohary 1966; Zohary 1973), where it grows in several steppe-like herbaceous formations in the *Quercus ithaburensis* and *Q. brantii* open-park forest belt (Nevo et al. 2002). Peripheral western populations are present in *Q. calliprinos* macquis or in the open park forest of *Ceratonia siliqua* (Nevo et al. 2002). Natural populations of wild emmer wheat in the catchment area of the Upper Jordan Valley are common, lush and continuous in their spread. However, elsewhere in the Fertile Crescent wild emmer wheat populations are semi-isolated or isolated, and display a patchy structure (Nevo et al. 2003). Johnson (1975) reported that from southeastern Turkey into Iraq and Iran the species is progressively substituted by another wild tetraploid wheat, *T. araraticum* (*T. araraticum* Jakubz.). In the same areas, occasional *T. dicoccoides* populations are reported to be present among stands of *T. araraticum* (Tanaka and Ishii 1973). *T. dicoccoides* and *T. araraticum* are morphologically very similar but not interfertile (Zohary and Hopf 2000). One further centre of massive stands of wild emmer are the basaltic rocky slopes of the Karacadag and Kartal mountain ranges in southeast Turkey (Harlan and Zohary 1966; Özkan et al. unpublished). The altitude of wild emmer habitats ranges from 100-150 m below sea level up to 1600-1800 m above sea level (Nevo et al. 2002). The wild species grows in very different climatic regions from cool and humid mountains like the Karacadag mountains to hot and dry valleys in southern Israel. The species needs at least 400 mm rainfall (Willcox 2005). Wild emmer is mainly restricted to primary habitats (Harlan and Zohary 1966; Nevo et al. 1982; 1984). However, at least in Turkey, it can also rarely colonize secondary habitats (Özkan et al. unpublished). The species is adapted to basaltic rocks but occurs also on hard limestone bedrocks, and on terra rossa soils (Nevo et al. 2002; Özkan et al. unpublished).

Wild emmer possesses two sets of homologous chromosomes, designated as AABB resulting from spontaneous hybridization between two wild diploid grasses, *T. urartu* (AA) as male and *Ae. speltoides* (SS = BB in wheat) as female donor (for review see Kilian et al. 2007). Recent data assume that this hybridization took place about 0.36 MYA ago (Dvorak and Akhunov 2005). Wild emmer wheat has been domesticated around 11,000 years ago by humans in the Fertile Crescent leading to domesticated emmer (*T. dicoccum*) which around 10,000-8,000 years ago was then involved in crosses with wild diploid *Aegilops tauschii*. This gave rise to the hexaploid bread wheat *T. aestivum* (summarized in Salamini et al. 2002). Evolutionary relationships between wheats with different ploidy levels are shown in Supplementary figure S2 of Kilian et al. (2007). Domesticated emmer wheat, *T. dicoccum*, has hulled seeds but a free-threshing form that releases seeds during threshing is known (hard wheat; *T. durum*). These two domesticated forms have a non-brittle rachis (the ear releases the seeds but stays intact during threshing), in contrast to the progenitor *T. dicoccoides* (the ears of which fall apart at maturity and thus cannot be threshed).

Domesticated emmer was the most important crop in the Fertile Crescent until the early Bronze Age and was then substituted by other tetraploid and hexaploid wheats (Zohary and Hopf 2000). Domesticated forms are present at several early Neolithic archaeological sites like Tell Aswad (10,800 BP, years before present), Abu Hureyra 2 (10,400 BP) and Cayönü (10,600 BP) (for review see Salamini et al. 2002 and Licherter 2007).

Over the last decade efforts have been made to understand the cereal domestication process in the Fertile Crescent, including the place of domestication and the wild species involved. Meanwhile, a consensus has been reached on the existence of a core area, within the Fertile Crescent, where western agriculture originated. This is a small region in southeast Turkey, including the Karacadag mountain range, where the closest wild relatives of einkorn, emmer, barley, rye, chickpea, and lentil were domesticated and here they still grow today (Ladizinsky 1985; Nesbitt and Samuel 1996; Lev-Yadun et al. 2000; Gopher et al. 2001; Bar-Yosef 2002; Salamini et al. 2002; Ozkan et al. 2005; Abbo et al. 2006; Licherter 2007). Only barley seems an

exception, because several studies published up to now point to barley domestication as having taken place in the Israel-Jordan region (Badr et al. 2000; Kilian et al. 2006).

Archaeological and molecular studies contributed equally but here we will focus on molecular studies. New molecular fingerprinting techniques to this scientific sector enable to screen large germplasm collections at several loci in order to understand crop domestication in detail. They have also shown the potential of wild cereals for crop improvement. The approach involves comparing wild and domesticated populations using molecular markers, which generates genome-wide estimates of genetic similarity (Heun et al. 1997; Badr et al. 2000; Martin and Salamini 2000).

In 1997 Heun et al. used the AFLP (amplified fragment length polymorphism) technique and compared 261 wild einkorn *T. boeoticum* (*T. boeoticum* Boiss.), still growing in the Fertile Crescent, and 68 lines of cultivated einkorn wheat, *T. monococcum* (*T. monococcum* L.) in order to identify the site of einkorn domestication. In this study, a genetically distinct group of 11 wild einkorn lines from the Karacadag mountain range in southeast Turkey was identified. The lines were more similar to cultivated einkorn than any other wild line studied. Therefore Heun et al. (1997) suggested the Karacadag mountain range in southeast Turkey as site of einkorn domestication. In 2000 Badr et al. while also using AFLPs, concluded that barley was domesticated in southern Levant. These two studies pioneered the search for the origin of crop domestication using large germplasm collections and considering many loci.

Ozkan et al. (2002) applied the AFLP technique in the search for the site of emmer domestication. A collection of 99 wild emmer wheat sampled from primary habitats at known locations throughout their whole distribution area and 43 domesticated emmer lines (19 hulled emmer landraces and 24 free threshing hard wheat lines) was studied, based on 204 nuclear AFLP marker loci. The most important findings were that 15 out of 19 lines from the Karacadag mountain range were more related to domesticated emmer and hard wheat than any other lines. Furthermore, hulled emmer (*T. dicoccum*) and *T. durum* (free-threshing) grouped separately on a Neighbor-joining tree, although the two groups merged into a common lineage soon before joining the wild emmer topologies. Therefore, Salamini et al. (2004) reported that a monophyletic or a diphyletic domestication of tetraploid wheat were possible. These findings supported that emmer was also domesticated in the Karacadag area.

In addition to this analysis, chloroplast (cp) DNA fingerprinting using microsatellite markers of wild and domesticated emmer wheat indicated that two distinct maternal lineages have been involved in the emmer domestication process, suggesting that the event occurred at least twice (Mori et al. 2003). A large number of cpDNA haplotypes could be detected within two broad lineages, I and II. Haplotype 10, belonging to lineage I, was present in 39.6% of domesticated emmer accessions and 90% of bread wheat (*T. aestivum*) accessions. This haplotype was present only in three accessions of wild emmer from the Kartal mountain region (280 km west of the Karacadag mountains). In addition, haplotypes 22 and 59 belonging to lineage II in domesticated emmer and bread wheat could not be found in wild emmer, but closely related haplotypes were encountered in geographically diverse populations of wild emmer. It was then concluded that emmer was domesticated twice, once in the Kartal mountain region and a second time somewhere else.

One year later, Ozkan et al. (2005) reconsidered the site of emmer domestication. A comprehensive collection of 224 lines was investigated (including 131 accessions from Ozkan et al. 2002, 69 accessions from Mori et al. (2003), 7 lines from B. Gill and 17 lines from A. Karagöz) and 169 nuclear polymorphic AFLP loci were scored. Phylogenetic analysis again indicates that the Karacadag population, intermixed with some lines from Iraq and Iran, has the highest similarity to domesticated genotypes, whereas the Kartal mountain population is less related to the domesticated gene pool. During this work two distinct genetic *T. dicoccoides* taxa were reported: The western race colonizing primary habitats in Israel, Jordan, Lebanon and Syria, and

the central-eastern race, frequently sampled in Turkey and rarely in Iraq and Iran. It remains open were these two races intersect (fig.1) Only the central-eastern race played a role as progenitor of domesticated emmer wheat.

The question of emmer domestication was than revisited by Luo et al. (2007) using restriction fragment length polymorphisms (RFLP) at 131 single copy loci in 277 accessions of wild emmer, 186 domesticated emmer landraces and 55 landraces of durum wheat. The aim was to describe again emmer domestication and its subsequent diffusion across Asia, Europe and Africa and to understand the population structure of wild and domesticated emmer in more detail. The authors confirmed that wild emmer consists of two genetically distinct populations each further subdivided. However, also domesticated emmer is divided into two populations. Gene flow between wild and domesticated emmer wheat occurred across the entire area of wild emmer distribution. Emmer was likely domesticated in the Karacadag region in southeastern Turkey, which was followed by subsequent hybridization and introgression from wild to domesticated emmer in southern Levant.

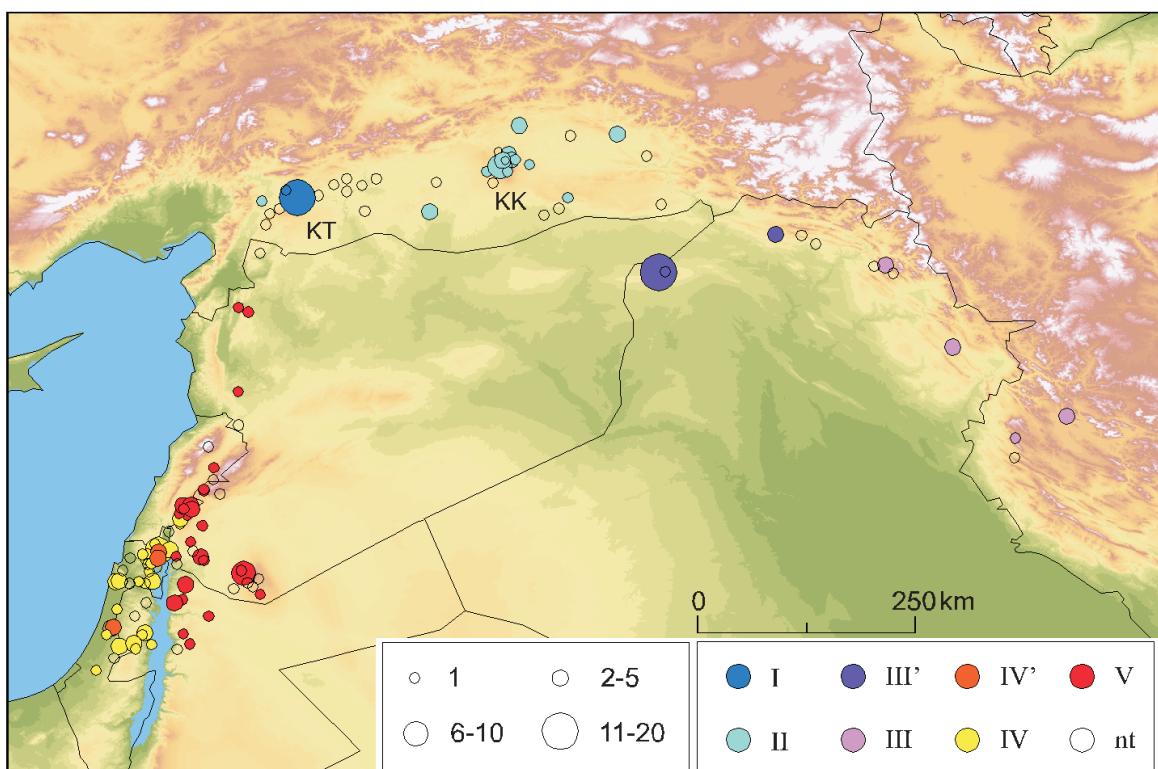


Fig. 1. - Natural distribution and region of wild emmer domestication. Geographical information system (GIS) based overview of wild emmer collection sites. Collection sites informations have been combined from Harlan and Zohary (1966), Johnson et al. (1975), Zohary and Hopf (2000), Nevo et al. (2002) and Ozkan et al. (2005) and recent observations from Ozkan et al. (unpublished) were included. Race assignments from genetic analyses based on Ozkan et al. 2005 are color-coded. The western race consists of three subgroups IV', IV and V. The central-eastern one comprises subgroups I, II, III' and III. Other wild emmer collection sites that are not included in Ozkan et al (2005) are shown without colour. Numbers of individuals collected at specific sites (Ozkan et al. 2005) are indicated by a key at the bottom. KK - Karacadag; KT - Kartal-Karadag. nt – not tested by Ozkan et al. (2005).

The transition from wild emmer to modern tetraploid wheats involved several changes in morphological traits and genome structure. The genome size has been reduced from about 12,000 MB in wild *T. dicoccoides* to about 11,785 Mb in domesticated *T. dicoccum* (Rees and Walther 1965). Furthermore, genes have been silenced or changed their function (Ayal et al. 2005). During these transitions major losses of natural diversity is thought to have occurred. In the most recent study, Haudry et al. (2007) analyzed 21 nuclear loci in 101

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individuals (28 *T. dicoccoides*, 12 *T. dicoccum*, 20 *T. durum* and 41 *T. aestivum*) to unravel evolutionary history and to quantify genetic diversity. The wild *T. dicoccoides* group was not highly polymorphic, no population structure could be detected and no significant correlation between genetic and geographic distances could be measured. During the transition from wild to domesticated wheat nuclear diversity was reduced in domesticated forms by 70% in *T. dicoccum*, 84% in *T. durum* and 69% in *T. aestivum*. The question remains open if this loss of nucleotide diversity occurred during the domestication process, which could have lasted up to one millennium in this region (Tanno and Willcox 2006), or later during subsequent intensive breeding.

Ongoing and future excavations in the core area like at Göbekli Tepe (Lichter 2007) and continued molecular studies will provide deeper insights into emmer domestication. At the molecular level the time has come to use and to sequence large germplasm collections in order to compare many wild and many domesticated individuals and populations per species at many loci. Such studies will provide more detailed insights into the natural variation present in wild and domesticated plants and will shed light upon the domestication process. That knowledge will, in turn, help us to improve our crops in a changing world.

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Chapter 6

Estimating genetic diversity in durum and bread wheat cultivars from Turkey using AFLP and SAMPL markers

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Abstract

Since 1925, more than 100 wheat varieties were developed and released in Turkey, and many more were introduced from abroad, but no systematic analysis of their genetic diversity has been performed yet. In this research, a total of 34 domestic and foreign cultivars (12 durum and 22 bread wheats), released in Turkey between 1936 and 2000, were fingerprinted by means of five AFLP and three SAMPL primer combinations, to evaluate their genetic variation and to determine the existence of cultivar-specific bands. Among the 344 amplicons scored, 214 were polymorphic. The primer combination E_{ACG}/M_{AGG} yielded the highest number and the primer combination SAMPL-6/ M_{AGA} produced the lowest number of polymorphic bands. Most cultivars were molecularly very similar, although a few distinct ones (the durum wheat Kunduru-1149 and the bread wheat Ikitce-96) were also identified. Seven cultivar-specific markers for different bread wheat cultivars (Golia, Seri-82, Adana-99, Pandas and Sertak-52) and six cultivar-specific markers for durum wheat cv Kunduru were observed. Our results show that genetic diversity among old and present-day wheat cultivar commonly grown in Turkey is limited.

Introduction

During the last 35 years wheat production in Turkey steadily increased, reaching about 21 million tons/year out of 9 million ha (the seventh largest area in the world). Meanwhile, genetic resources from Turkey contributed greatly to the increase of wheat production in many countries. Germplasm exploration and collection missions led to the evaluation of sampled materials in different countries, and several landraces (e.g. Turkey Red) were largely utilized to breed new varieties. In Turkey modern wheat breeding started in 1925: its main goal was to select, from local population, lines adapted to the different regions of the country. This breeding effort quickly produced cultivars such as Yayla-305 and Ak-702 (Gökgöl 1939). In 1967 the National Wheat Release and Training Project was established, with the contribution of international organizations, resulting in the Turkish Green Revolution. Since then many cultivars were introduced from foreign countries, specifically targeting different areas. The national breeding program, meanwhile, developed over 100 wheat cultivars, most of which had a significant impact on the economy.

Information on germplasm diversity and genetic relationships among cultivars are critical in wheat improvement. Genetic similarities might be evaluated by means of pedigree analysis (Barrett et al. 1998) or by assessing morphological traits (Schut et al. 1997) as well as biochemical (Metakovski and Branlard 1998) or, more recently, DNA markers (Barrett et al. 1998; Pagnotta et al. 2005). DNA markers are useful complements to the morphological and physiological characterization of cultivars because they are plentiful, are not influenced by plant tissue or environmental effects, and allow cultivar identification very early in plant development (Manifesto et al. 2001). Today, DNA markers are largely employed in diversity studies, following different techniques such as RFLP (Kim and Ward 1997; Paul et al. 1998), RAPD (Sun et al. 1998), sequence-tagged site PCR (STS-PCR) (Chen et al. 1994), AFLP (Barrett and Kidwell 1998; Burkhamer et al. 1998), SAMPL (Roy et al. 2002) and SSR (Plaschke et al. 1995).

The amplified fragment length polymorphism (AFLP) technique (Vos et al. 1995) detects high levels of DNA polymorphism and is extremely promising for fingerprinting, mapping and genetic diversity studies. One of its main advantages is the high multiplex ratio, which means that large numbers of amplified products are generated in a single reaction (Powell et al. 1996). Furthermore, reproducibility, heritability and intra-specific homology of AFLPs have already been demonstrated (Mackill et al. 1996).

Selective amplification of microsatellite polymorphic loci (SAMPL), a microsatellite-based marker system, is a modification of the AFLP methodology (Roy et al. 1996): it differs in that the selective amplification is achieved using one AFLP primer in combination with one SAMPL primer (Rakoczy-Trojanowska and Bolibok 2004). The use of a SAMPL primer in combination with an AFLP primer is particularly suitable when low genetic variation is expected, since the primers target the hyper-variable microsatellite loci (Witsenboer et al. 1997).

So far, the genetic diversity of Turkish-grown wheat cultivars is not well understood. Objectives of this work were therefore (I) to characterize by AFLP and SAMPL markers twelve durum wheat and twenty-two bread wheat cultivars, old and modern, grown in Turkey; (II) to determine the existence of cultivar-specific amplicons; (III) to assess the relative informativeness of AFLPs and SAMPLs.

Materials and Methods

Plant material

A total of thirty-four wheat cultivars, including 12 durum (*Triticum turgidum* ssp. *durum*) and 22 bread (*T. aestivum* ssp. *aestivum*) wheat cultivars, most of them bred in Turkey during the last 70 years were fingerprinted in this study. Name/pedigree of the cultivars are presented in table 1.

DNA extraction and AFLP / SAMPL analyses

Leaf samples were collected from each cultivar, frozen in liquid nitrogen and stored at -70°C until use. Genomic DNA was extracted from leaf tissue by the CTAB method of Doyle and Doyle (1987) with minor modifications (Kafkas et al. 2005). The AFLP and SAMPL amplifications were performed according to Vos et al. (1995), with minor modifications (Ozkan et al. 2005), using five AFLP primer combinations (E_{ACG}/M_{AGC} , E_{ACG}/M_{ACC} , E_{ACG}/M_{ACT} , E_{ACG}/M_{AGG} , E_{ACG}/M_{AGT}) and three SAMPL primer (5'-ACACACACACACACATATAA-3') combinations (SAMPL6/ M_{AGA} , SAMPL6/ M_{ATA} , SAMPL6/ M_{ATG}).

A total of 10 µl of the AFLP and SAMPL selective amplification product was mixed with 10 µl of loading buffer, denatured at 94 °C for 5 min and placed on ice. After a pre-run electrophoresis at 60 W for 30 min, about 3 µl of mixture were loaded onto a 4.5 % (w/v) polyacrylamide denaturing gel with 0.5X TBE buffer and run at 60 W until the loading dye reached the bottom of the gel. The gels were dried at 80°C for 3 h; an autoradiographic Hyperfilm-MP (Amersham, England) was exposed to the gels for 2 days.

Band Scoring and Data Analysis

The AFLP and SAMPL bands were visually scored as present (1) or absent (0): only the clearest and strongest bands were recorded and used for the analysis. The bands were independently scored twice, by two different observers. The ability of the most informative primer pairs to differentiate between genotypes was assessed by calculating their resolving power (Rp) according to Prevost and Wilkinson (1999) using $Rp = \sum I_b$, where I_b is band informativeness and $I_b = 1 - [2 \times (0.5 - p)]$, where p is the proportion of genotypes containing band.

Genetic distances were calculated by the PAUP 4.0b program (Swofford 1998) according to the method developed by Nei and Li (1979). These distances were used to build an unweighted pair-group method with arithmetic means (UPGMA) tree. Principal Components Analysis (PCA) was carried out using the NTSYS-pc 2.11 software (Rholf 1993).

Table 1. Name, year of release, pedigree and origin of the 34 wheat cultivars used in this study

Cultivars	Year	Pedigree	Origin
<i>T. turgidum</i> ssp. <i>durum</i>			
Dicle-74	1975	Rojo AlicanteE/4*Tehuacan60//Stewart63/3/(S)	Mexico
Gediz-75	1976	LD357E/TC2//Jori”S”	Mexico
Diyarbakır-81	1981	LD393//BEL116E/2*TC/3/CIT71	Turkey
Harran-95	1995	Korifla//D.S-15/Geiger	Turkey- Mexico
Ceylan-95	1995	STORK”S”/RABI”S”	Turkey- Mexico
Saricanak-98	1998	DACK/GEDIZ//USPA575	Turkey- Mexico-Syria
Kunduru-1149	1967	Landrace	Turkey
Çakmak-79	1979	UVY162/61.130	Turkey
Balcalı-2000	2000	Stn “S”	Turkey
Balcalı-85	1985	Bittern “S”	Turkey
Amanos-97	1997	-	Turkey
Selçuklu-97	1997	073-44*2/Ovi/3/DF21-72//61-130/Uvy162	Turkey
<i>T. aestivum</i> ssp. <i>aestivum</i>			
Gerek-79	1979	MEN’S’//MY48/4-11/3/YY305	Turkey
Atay-85	1985	Hyslop/7Cerros66	Turkey
Katia-I	1990	Chebros/BEZ	Bulgaria
Gün-91	1991	F35.70/Mochis73	Turkey-Mexico
Da□da□-94	1994	093-44/AU//SIHHE	Turkey
Kutluk-94	1994	KSК//INIA/LFN/3/Çalibasan	Turkey
Pehlivان	1995	BEZ/TUR/5/CFN/BEZ	Turkey
Kirgiz-95	1995	Domanic*2/AU	Turkey
Ikizce-96	1996	ATR*2/7C//BL	Turkey
Pandas	1984	Orso//BEZ-1/S1/GEN7/Marzotto	Italy
Seri-82	1992	Vee”5”	Turkey-Mexico
Kasifbey-95	1995	PFAU”S”	Turkey-Mexico
Golia	1989	Manital/Orso	Italy
Gönen-98	1998	8156/Mara//BB	Turkey
Kıraç-66	1966	Florence/Yayla305	Turkey
Bolal	1970	Cheyenne/Kenya/Mentana	USA
Sertak-52	1936	Landrace	Turkey
Nurkent	-	-	Turkey
Genç-88	1988	“Cno””S’/Nac//Cc//Inia/3/Bb/Nar59”	Turkey
Yayla-305	1939	Landrace	Turkey
Bezostaya	-	-	Russia
Adana-99	1999	PFAU/Seri-82/BOW	Turkey-Mexico

Cultivars Name of cultivars
Year Year of release

Results

Five AFLP and three SAMPL primer combinations were used to characterize 12 durum wheat and 22 bread wheat cultivars. Out of a total of 344 amplicons, 214 (62%) were polymorphic, averaging 43 total bands and 26.8 polymorphic bands per primer combination (table 2). The five AFLP primer sets amplified 251 bands (64% of them polymorphic), with an average of 50.2 total and 32 polymorphic bands per primer pair. In SAMPL analysis, the three primer combinations amplified 93 bands (58% of them polymorphic),

Table 2. Number of total and polymorphic bands, percentage of polymorphism, and resolving powers of primer pairs detected in the DNA fingerprinting of 14 durum and 20 common wheat cultivars with AFLP and SAMPL markers

Primer Comb.	Durum and Common Wheat				Durum Wheat				Bread Wheat			
	Total	Poly-morphic	P (%)	(Rp)	Total	Poly-morphic	P (%)	(Rp)	Total	Poly-morphic	P (%)	(Rp)
E _{ACC} / M _{AGC}	45	27	60	29.1	44	24	54	24.6	45	26	58	30.2
E _{ACG} / M _{ACC}	49	27	55	33.6	47	12	26	10.6	49	17	35	19.9
E _{ACG} / M _{ACT}	57	34	59	40.8	53	18	34	17.6	57	29	51	35.5
E _{ACG} / M _{AGG}	55	42	76	54.1	55	21	38	24.3	55	31	56	45.5
E _{ACG} / M _{AGT}	45	30	67	42.2	44	23	52	20.0	45	18	40	25.0
Subtotal	251	160	64		243	98	40		251	121	48	
Average	50.2	32			48.6	19.6			50.2	24.2		
SAMPL6 / M _{AGA}	30	16	53	25.1	30	10	33	10.2	30	11	37	19.8
SAMPL6 / M _{ATA}	30	18	60	23.1	30	12	40	10.7	30	12	40	15.6
SAMPL6 / M _{ATG}	33	20	61	28.3	33	19	58	26.8	33	19	58	26.0
Subtotal	93	54	58		93	41	44		93	42	45	
Average	31.0	18			31.0	13.7			31	14.0		
TOTAL/	344	214	62		336	139	39		344	163	47	
AVERAGE	43.0	26.8			42.0	17.4			43.0	20.4		

P Polymorphism
Rp Resolving power
Total Total no. bands
Polymorphic No. polymorphic bands

with an average of 31 total and 18 polymorphic fragments. The individual primer pairs produced between 30 and 57 bands, while the percentage of polymorphism per primer combination ranged from 53% to 76%. The same trend is observed also within species: in durum wheat polymorphism varied between 26% and 58% (mean 39%), while in bread wheat varied from 35% to 58% (mean 47%). The average number of total and polymorphic bands was slightly lower in durum wheat compared to bread wheat.

The resolving power (Rp) of the different primer combinations (table 2) ranged between 23.1 and 54.1 (durum wheat: 10.2-26.8; bread wheat: 15.6-45.5). According to the Rp values of all primer combinations, the AFLP primers discriminated the 34 wheat cultivars better than the SAMPL primers.

The UPGMA dendrogram (fig.1) clearly split wheat cultivars according to their species/ploidy: subcluster I gathered all *T. turgidum* (AABB) and subcluster II grouped all *T. aestivum* (AABBDD). Within species, cluster I was divided into three sub-clusters: IA (eight genotypes), IB (three genotypes) and IC (only Kunduru-1149); the eight durum wheat cultivar of sub-cluster IA were further divided into two groups, one with five genotypes and the other one with three genotypes. Cluster II was also divided into three clusters: IIA (19 genotypes), IIB (two genotypes) and IIC (only one genotype, cv. Ikizce). The 19 common wheat cultivars of sub-cluster IIA were further divided in two groups, one with 9 genotypes and the other one with 10 genotypes. To test the goodness of fit of the UPGMA cluster analysis on our AFLP and SAMPL datas, the MxComp routine in NTSYS-pc was used to compute the cophenetic value. The correlation r=0.925, obtained for the UPGMA method, suggests a very good fit of the original data with the final dendrogram.

The principal components analysis results are depicted in fig. 2. The first three components of PCA accounted for 44.79% of total variation and the 34 genotypes were well separated into two groups, according

to ploidy level. Kunduru-1149 (durum wheat) and İkizce-96 (bread wheat) were clearly different from the other cultivars.

The average pair-wise genetic distance (proportion of different bands) among all genotypes was 0.128, ranging from 0.013 to 0.357 (data not shown). The average genetic distance between durum wheat and bread wheat cultivars was 0.304. In durum wheat the mean was 0.132, varying from 0.072 (Saricanak-Balcalı-85) to 0.216 (Selçuklu-Kunduru-1149), while in bread wheat the mean was 0.127, ranging from 0.066 (Genc-88-Nurkent) to 0.214 (Dagdas-İkizce).

Discussion

AFLP and SAMPL have been extensively used as molecular marker systems for detecting DNA polymorphism in wheat. In this study, the use of five AFLP and three SAMPL primer pairs resulted in polymorphism ranging from 53% to 76%, high levels when compared to previous studies: for example, Barrett and Kidwell (1998) found 11.8% polymorphisms among 54 genotypes, using 16 primer pairs; Roy et al. (2002) found 49.4% polymorphisms among 55 wheat cultivars; Hazen et al. (2002) detected 23.2% polymorphisms in 44 genotypes, using 8 primer pairs; Bohn et al. (1999) reported 21.0% of polymorphism with 11 wheat genotypes, using 11 primer pairs. However, genotypes and primer pairs in the above-mentioned researches were different, making the results not easily comparable.

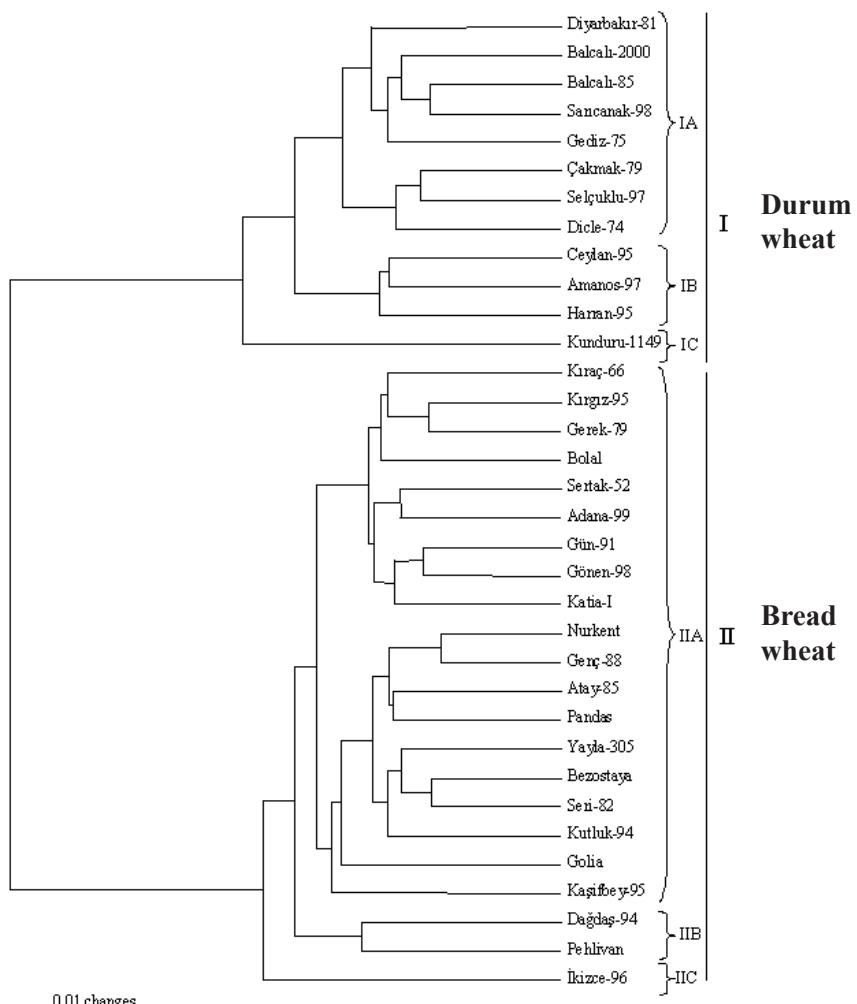


Fig. 1. - UPGMA dendrogram of 12 durum and 22 bread wheats from Turkey.

The efficiency of the different marker techniques for estimating DNA polymorphism in wheat is variable. For instance, Joshi and Nguyen (1993), among 15 wheat cultivars, used 40 RAPD primers and observed 1.8 polymorphic bands per primer, while, Sun et al. (1996) detected seven polymorphic bands per primer analyzing 46 genotypes of *T. aestivum* and *T. spelta* with 26 RAPD primers. For RFLPs, the number of polymorphic bands per probe/enzyme combination in bread wheat ranged from 1.2 in 222 genotypes (Kim and Ward 1997) to 3.3 in 124 cultivars (Paul et al. 1998). ISSR primers detected 3.7 polymorphisms per primer (Nagaoka and Ogiwara 1997), while microsatellites were more polymorphic, with 6.2 alleles/bands (Plaschke et al. 1995). SAMPL primer pairs detected 21.5 polymorphisms per primer pair in 55 wheat cultivars (Roy et al. 2002). In our study, using only five AFLP and three SAMPL primer pairs, we observed 344 fragments, with an average of 26.8 polymorphic loci per primer pair (17.4 among durum wheat cultivars and 20.4 among bread wheat cultivars). Therefore, they detected at least three to four times more polymorphisms per primer pair than any other molecular marker technique. Thus AFLP, alone or combined to SAMPL, is probably the most efficient marker system also in the case of wheat.

Seven cultivar-specific markers for bread wheats and six cultivar-specific markers for durum wheat cultivars were found among the 214 polymorphic bands observed. In bread wheat the cultivar-specific fragments were distributed between five different cultivars (Golia, Seri-82, Adana-99, Pandas and Sertak-52). In durum wheat, however, they were all restricted to Kunduru-1149. If these findings are confirmed over a broader range of accessions, the unique bands could be useful for the identification of these six cultivars, directly or after development of sequence-tagged site primers.

A poor agreement between the AFLP/SMPM clustering and the available pedigree informations is evident for both species. For example, Katia-I and Pehlivan share one common parent, but consistently appear in different sub-clusters. It has to be remembered that low to moderate correlations between genetic diversity estimations based on pedigree analysis and on RAPD data were reported for bread wheat (Kudlyavtsev et al. 2003; Sun et al. 2003), although Barrett et al. (1998) reported that genetic distances for AFLP based on enzyme combination *PstI/MseI* were better correlated with pedigree than estimations based on *EcoRI/MseI*.

Our data seem to indicate a low genetic diversity among the wheat cultivars cropped in Turkey. This observation agrees with the results of Chao et al. (1989), Devos and Gale (1992) and Shoaib and Arabi (2006). However, Burkhamer et al. (1998), using AFLPs, found a genetic similarity of 0.55 (range from 0.34 to 0.81) in a pool of 10 hard red spring wheat cultivar. The narrow genetic basis of modern wheat cultivars is well known and demonstrated by both pedigree (Cox et al. 1986) and molecular analysis (Chen et al. 1994; Sun et al. 1996).

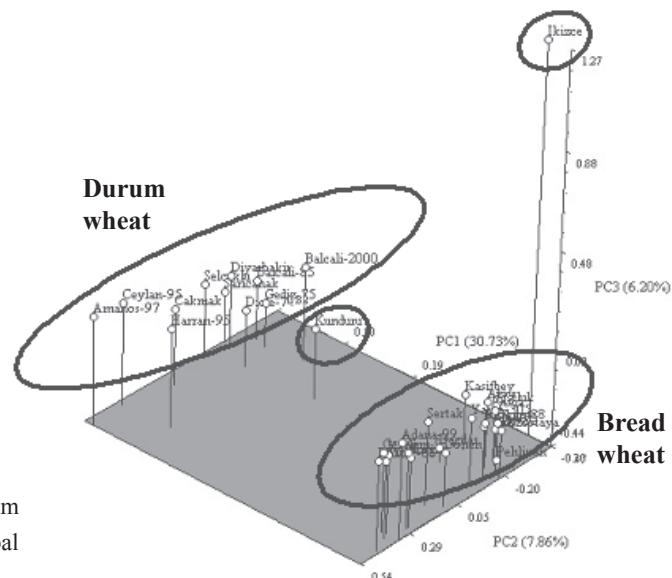


Fig. 2. - Patterns of relationship among 12 durum and 22 bread wheats cultivars as revealed by Principal Component Analysis based on AFLP and SAMPL data.

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Most of the Turkish wheat cultivars used in this study were bred, directly or indirectly, from CIMMYT germplasm. Actually, only three wheat cultivars trace back exclusively to Turkish landraces (durum wheat Kunduru and bread wheats Sertak-52 and Yayla-305). This suggests that old Turkish cultivars have scarcely been included within the genetic pool used for breeding modern varieties and highlights the primary role of the germplasm developed by CIMMYT.

Our results have relevant implications for Turkey wheat breeding. First, present day commonly-grown Turkish wheat cultivars have a narrow genetic diversity, most likely as the results of selection pressure and genetic drift in breeding programs. The genetic relationships observed among these cultivars, therefore, are helpful for current and future breeding programs in order to select genetically distinct parents. Second, the narrow genetic diversity observed among Turkish wheat cultivars suggests the need of broadening the genetic base of wheat breeding materials, including local landraces. This is even more relevant since Dreisigacker et al. (2004), Karagöz and Zencirci (2004) and Zencirci and Karagöz (2005) reported that some Anatolian wheat landraces host a broad genetic diversity, an observation substantiated also by our study: Kunduru, the most diverse durum wheat cultivar, was directly selected from a landrace. This study shows that the Turkish landraces of durum and bread wheat are quite unique and markedly differ from other wheat germplasm. Further surveys are urgently needed to elucidate the genetic structure of the Turkish wheat genepool and to identify new useful alleles.

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Chapter 7

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

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Abstract

The diploid wheat *Triticum monococcum* L. (einkorn) was among the first crops domesticated by humans in the Fertile Crescent 10,000 years ago. During the last 5,000 years it was replaced by tetraploid and hexaploid wheats and largely forgotten by modern breeders. Einkorn germplasm is thus devoid of breeding bottlenecks and has therefore preserved in unfiltered form the full spectrum of genetic variation that was present during its domestication. We investigated haplotype variation among >12 million nucleotides sequenced at 18 loci across 321 wild and 92 domesticate *T. monococcum* lines. In contrast to previous studies of cereal domestication, we sampled hundreds of wild lines, rather than a few dozen. Unexpectedly, our broad sample of wild lines reveals that wild einkorn underwent a process of natural genetic differentiation, most likely an incipient speciation, prior to domestication. That natural differentiation was previously overlooked within wild einkorn, but it bears heavily upon inferences concerning the domestication process because it brought forth three genetically, and to some extent morphologically, distinct wild einkorn races that we designate here as α , β , and γ . Only one of those natural races, β , was exploited by humans for domestication. Nucleotide diversity and haplotype diversity in domesticate einkorn is higher than in its wild sister group, the einkorn β race, indicating that einkorn underwent no reduction of diversity during domestication. This is in contrast to findings from previous studies of domestication history among more intensely bred crop species. Taken together with archaeological findings from the Fertile Crescent, the data indicate that a specific wild einkorn race that arose without human intervention was subjected to multiple independent domestication events.

Introduction

Archaeological evidence indicates that western agriculture began in the Near East with the remains of founder crops preserved at several excavated sites throughout the region known as the Fertile Crescent (Heun et al. 1997; Moore et al. 2000; Zohary and Hopf 2000; Gopher et al. 2001; Salamini et al. 2002). Beginning about 12,000 years ago, the size and morphology of archaeologically preserved einkorn seeds (*Triticum monococcum*, genome AA with 2n=14) changed, with the smaller seeds of wild einkorn (*Triticum monococcum* ssp. *boeoticum*, *T.m.b.*) gradually being replaced at excavated sites by the larger seeds of its domesticate form (*Triticum monococcum* ssp. *monococcum*, *T.m.m.*) (Zohary and Hopf 2000) and genetic data for einkorn is consistent with that view (Heun et al. 1997; Abbo et al. 2006). In crop grasses of the Fertile Crescent — wheats, barley, and rye — domestication is currently thought to mainly involve allele frequency changes at loci governing seed size, rachis stiffness and bract morphology (Salamini et al. 2002), but the mechanisms through which humans evoked those morphological changes are still debated.

Evidence from archaeological excavation sites indicates that the process of crop domestication spanned up to 1000 years and entailed multiple domestication events (Willcox 1999; Hillman and Davies 1990; Kislev 2002; Salamini et al. 2002; Tanno and Willcox 2006). Such evidence stands contrary to molecular studies that have suggested a single domestication of each of the Fertile Crescent founder crops (Heun et al. 1997; Badr et al. 2000; Zohary and Hopf 2000). A third view of domestication suggests that superior varieties emerged in a core area and were then dispersed throughout the region, displacing local genotypes (Lev-Yadun et al. 2000; Salamini et al. 2002; Abbo et al. 2006). All of these models predict a reduction of genetic diversity in domesticate forms relative to the wild progenitors through a domestication bottleneck — a reduction in genetic diversity stemming from human selection upon domestication traits — as reported in various

domesticated species (Pozzi et al. 2004; Doebley et al. 2006; Kilian et al. 2006). However, distinguishing between reduction of genetic diversity through a domestication bottleneck introduced over 10,000 years ago and reduction through intensive breeding bottlenecks during the last few hundred years is extremely problematic (Kilian et al. 2006), and domestication genetic studies of Old World crops that escaped intense breeding are lacking.

Einkorn is unique in this respect because it was of limited agricultural use during the last 5,000 years: the crop was largely abandoned as a foodsource starting in the Bronze Age, and intensive breeding was never undertaken (Salamini et al. 2002). As a consequence, domesticate einkorn germplasm sampled in remote mountain areas across Europe and the Near East (Perrino et al. 1996) should harbor a representative sample of Neolithic genetic variation that was present during domestication in the Fertile Crescent and that was later dispersed by migrating farmers (Nesbitt and Samuel 1996). Given the absence of breeding bottlenecks in einkorn, we reasoned that extensive sampling of genetic diversity among wild and domesticate accessions should discriminate between competing hypotheses for cereal domestication. Here we report nucleotide variation at 18 loci for 92 domesticate einkorn lines in comparison to 321 lines from wild populations and a genetic view of crop domestication that is unbiased by green revolution breeding.

Methods

Plant material

Details of collection sites, taxonomic designations, seed sources, and seed bank accession numbers for the 603 lines used for amplified fragment length polymorphism (AFLP) analysis in figure 2A are given in Supplementary table S1. The same information for the 452 lines used for amplification and sequencing at 18 loci are given in Supplementary table S2.

AFLP analysis

DNA was isolated from freeze-dried or silica-dried leaves using the Qiagen (Hilden, Germany) DNeasy Kit, and amplified as described by Zabeau and Vos (1993) using the following primer combinations described in Heun et al. (1997): E_{ACC}/M_{ACC} (E36/M36), E_{ACG}/M_{AGC} (E37/M40), E_{AGC}/M_{ACT} (E40/M38), E_{AGC}/M_{AGC} (E40/M40), E_{AGT}/M_{AAC} (E42/M32), E_{AGT}/M_{AAG} (E42/M33), E_{AGT}/M_{ACT} (E42/M38). The AFLP bands were scored as binary data. NeighborNet planar graphs of AFLP Dice distances (Dice 1945) between individuals were constructed with SplitsTree 4.6 (Huson and Bryant 2006).

Multilocus genotype analysis

DNA was prepared as for AFLP analysis. PCR amplifications were performed in 25 µl containing ~100 ng of single leaf DNA, 0.4 µM of each primer, 125 µM of each dNTP (AB gene, Surrey, UK), 3 mM MgCl₂, 4% DMSO and 1 unit of *Taq* DNA polymerase incubated in a PTC-225 Tetrad Thermal Cycler (MJ Research). The loci are described in Supplementary table S3. Primers and specific amplification conditions for each locus are given in Supplementary table S4. PCR products were sequenced on both strands. Sequence data were processed with Applied Biosystems DNA Sequencing Analysis Software 5.1.1 and manually edited with BioEdit version 7.0.5.3 (Hall 1999). Alignments were generated with ClustalW, haplotypes were scored manually. Haplotypes were coded as discrete character data. NeighborNet planar graphs (Huson and Bryant 2006) of Hamming distances between 267 nonredundant multilocus genotypes among 452 individuals were

constructed based on haplotypes at 16 sequenced nuclear loci (without *Lr10*) and the chloroplast locus *ndhF*. GenBank accession numbers for the haplotypes determined at all 18 loci are reported in Supplementary table S5. Nucleotide diversity (π), haplotype diversity (Hd) and Watterson θ (Watterson 1975, equation 1.4a, but on base pair basis; Nei 1987, equation 10.3) were calculated using DnaSP version 4.10.9 (Rozas et al. 2003).

Topographic map

Void-filled seamless Shuttle Radar Topographic Mission (SRTM) data V1, 2004 (International Centre for Tropical Agriculture (CIAT), available from the CGIAR-CSI SRTM 90 m Database (<http://srtm.csi.cgiar.org>) were used to draw the topographic map. Global Positioning System (GPS) coordinates for collected and seed bank material are given in Supplementary tables S1-S2.

Median Joining networks

MJ networks (Bandelt et al. 1999) were constructed with the Network 4.2.0.1 program (Fluxus Technology Ltd., Clare, Suffolk, UK).

Morphological character analysis

Heading date, stem plus ear length excluding awns, and leaf sheath-to-ear tip distance for 341 lines (α (204 lines), β (11), γ (45), ae (6), M (70) and U (5)) were determined for plants grown in Cologne, Germany and San Angelo Lodigiano, Italy.

Statistical analysis

Because none of the morphological characters fitted a normal distribution (using Kolmogorov-Smirnov test for normality), we were restricted to use non-parametric statistical tests in our analysis. The distributions of the morphological characters were compared among the haplotypes by using the Wilcoxon non-parametric test (Zar 1999). In addition, we used the Bonferroni correction for multiple comparisons, that is, for three characters we used $\alpha=0.05/3=0.0167$ for the 95% significance level. Because nucleotide diversity also did not follow a normal distribution, we used the Friedman non-parametric test (Friedman 1937) to compare its distribution within loci among the different haplotypes.

Results and Discussion

Natural diversification and distinct wild races

We first investigated at 151 AFLP loci 603 diploid *Triticum* lines including 436 wild *T.m.b.* lines that cover the full range of wild einkorn dispersal (fig. 1), plus 70 domesticate *T.m.m.* lines, seven *T.m.* ssp. *aegilopoides* lines (*T.m.ae.* feral forms of *T.m.m.*), and 90 lines of *T. urartu* (the closest outgroup to *T. monococcum* within the genus). That coarse-grained, but genome-wide, survey uncovered an unexpected level of natural genetic differentiation among morphologically wild einkorn (fig. 2A). Genetic differentiation among these wild einkorn races, that we designate here as α , β , and γ , is not readily attributable to geographical separation (allopatry): although race α predominates in the Fertile Crescent and γ predominates in western and north-western Turkey, the wild races have overlapping ranges (fig. 1A), with race β occurring only in restricted areas of the Karacadag (KD) and Kartal-Karadag (KT) mountains, but together with race α (fig.

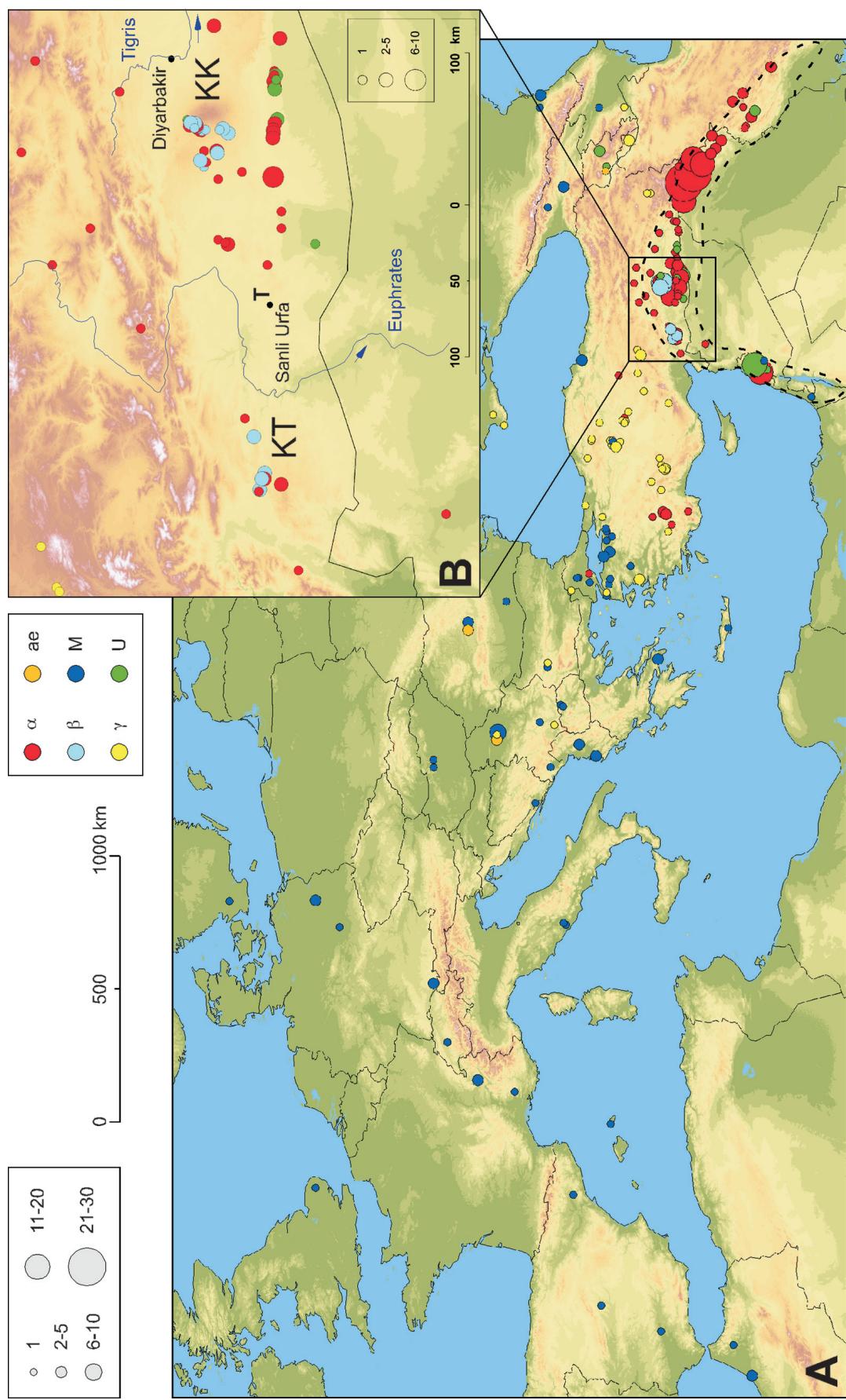


Fig. 1. - Natural distribution and region of einkorn domestication. (A) Geographical information system (GIS) based overview of the collection sites for accessions sequenced in the present study (Supplementary table S2). Race assignments from genetic analyses are color-coded: red - *T.m.b.* race α ; light blue - *T.m.b.* race β ; yellow - *T.m.b.* race β ; orange - feral form *T.m.ae* (αe); blue - domesticate *T.m.m.* (M); green - *T.urartu* (U). The Fertile Crescent is indicated with a dotted line. Numbers of individuals collected at specific sites are indicated by the key at upper left. (B) Enlargement of the region where *T.m.b.* race β occurs. Colors as in (A). KK - Karacadag; KT - Kartal-Karadag; T - Göbekli Tepe archaeological site (Schmidt 2001). For 55 lines (3 *T.m.b.* race α , 7 *T.m.ae*, 39 *T.m.m.*, 6 *T.urartu*) obtained from seed banks, the precise collection site is unknown and the capital city of the source country was arbitrarily chosen as collection site.

1B). At these 151 AFLP loci, race β is more closely related to domesticate einkorn (*T.m.m.*) and to its feral form (*T.m.ae.*) from the Balkan peninsula than the other wild races are (fig. 2A).

To get a more detailed picture, we investigate haplotypes for 321 wild *T.m.b.* lines representative for genome diversity at AFLP loci, 84 domesticate lines (European, Asian and Northern Africa collections), eight *T.m.ae.* lines from Southeast Europe and 39 lines of *T.urartu*. For each line, we sequenced 17 nuclear loci and one chloroplast locus (table 1), uncovering 415 single nucleotide polymorphisms (SNPs) and between two (*ndhF*) to 20 (6SFT) distinct haplotypes per locus within all lines sampled (including *T.urartu*). Einkorn is a typical inbreeder, but occasional outcrossing is observed (Zohary and Hopf 2000), also in the present data. Among 452 lines, 425 were homozygous at all loci sampled, only four were heterozygous at more than two loci, and 99.4% of all loci sampled were homozygous. In total, we surveyed >15,500 alleles amounting to >12 Mb of sequence data. Among the 452 lines, 322 contained unique haplotype combinations. The wild races α , β , and γ are distinct and are characterized by 23, 10, and 18 race-specific haplotypes, respectively (table 1). *T.urartu*, which can be morphologically distinguished from einkorn only in anther length, flowering time, and leaf trichomes (Morrison 1993), harbours an even more distinct haplotype collection. These distinctions are reflected in the network of multilocus genotype differences shown in fig. 2B.

The somewhat intermediate position of race γ between races α and β in the AFLP and multilocus genotype networks of fig. 2 might tend to suggest that it could be an α - β hybrid. However, the presence in race γ of 18 haplotypes that are specific to race γ and that are absent in races α and β (table 1) indicates the contrary. The distributions of three phenotypic characters (heading date, stem plus ear length excluding awns, and leaf sheath-to-ear tip distance) also distinguish race γ from α and β at $p << 0.01$ using the Wilcoxon non-parametric test with Bonferroni correction for multiple comparisons (fig. 3). We also found higher levels of haplotype and nucleotide diversity across loci in race γ than in race α (table 2). Race γ is thus the genetically most diverse of the three wild races. It is distinct from α and β , and it is morphologically wild, in line with the view that the natural dispersal range of *T.m.b.* includes western Turkey (Harlan and Zohary 1966, Johnson and Dahliwal 1976, Zohary and Hopf 2000) as indicated in fig. 1. *T.urartu* has far lower nucleotide diversity than einkorn wheat (table 2).

Taken together, the AFLP and haplotype data indicate that the wild α , β , and γ *T.m.b.* races are undergoing natural genetic diversification and that the process of genetic isolation has gone nearly to completion in the case *T.urartu*. The significance of this natural diversification is that it appears to have brought forth the β race upon which einkorn domestication at the origin of agriculture in the Fertile Crescent was built.

Nucleotide diversity, π , varies by orders of magnitude and in a locus-specific manner in the present einkorn data (fig. 4). This is in contrast to the observations in maize (Tenaillon et al. 2004), which is an outbreeder, but consistent with observations in another selfing species, *Arabidopsis thaliana* (Schmid et al. 2005). As seen in Median Joining (MJ) networks (fig. 5), for loci with low variability, one (*VRN1* and *BADH*, fig. 5K, *P*) or two (*ACCI* and *CesA*, fig. 5C, *H*) major haplotypes predominate, with a divergent haplotype present in *T.urartu*. For more variable loci, such as *pinB*, haplotypes differing by 10-20 nucleotide differences or more are distributed across all races, with *T.urartu* remaining distinct (fig. 5I). For *RGA2*, the most variable locus, haplotypes differing by more than 40 nucleotide differences are dispersed across wild and domesticate einkorn, with *T.urartu* remaining nearly monomorphic (fig. 5R). Taken together, the haplotype data indicate that these inbreeding wild einkorn races have sequestered haplotype diversity present in their common ancestor, that this diversity has been vertically preserved in the modern forms, and that a severe population bottleneck (of irrelevant nature in the present context) has eliminated allelic diversity in the wild outgroup *T.urartu*. In *T.urartu*, genetic diversity is primarily determined by the fixation of newly

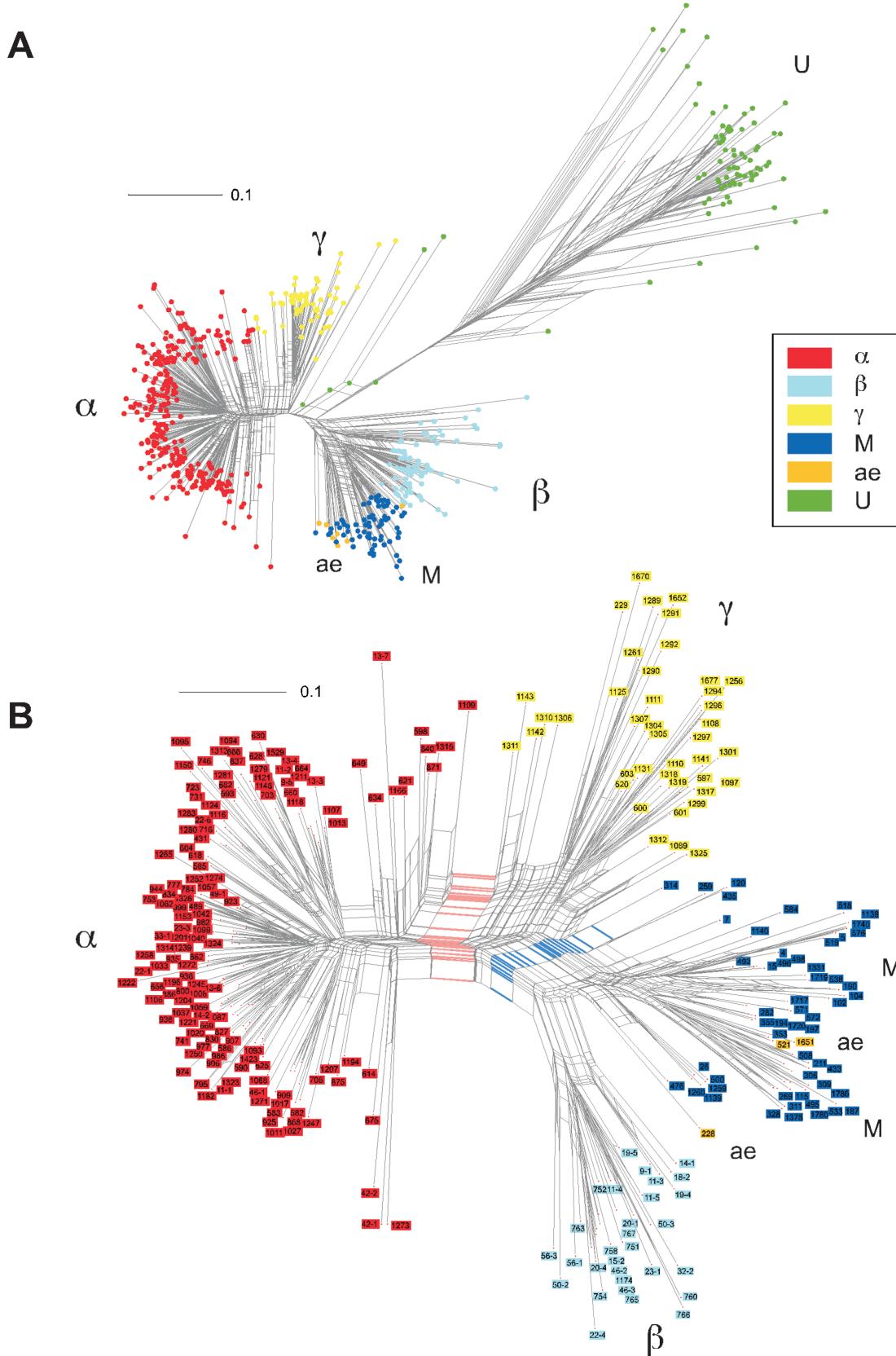


Fig. 2. - Genetic diversity among einkorn wheats and its sister species, *T. urartu*. **(A)** Phylogenetic network of 603 wheat individuals based on 151 AFLP chromosome markers. Details of the 603 *Triticum* lines used in this study are listed in Supplementary table S1. The AFLP data circumscribe 436 wild *T.m.b.* lines (races α , β , γ), 70 domesticated *T.m.m.* (M) lines, seven *T.m. aegilopoides* (ae) lines and 90 *T. urartu* (U) lines. **(B)** NeighborNet of 267 nonredundant multilocus genotypes among 452 individuals (Supplementary table S2, Supplementary Material online) based on haplotypes at 16 sequenced nuclear loci (without *Lr10*) and the chloroplast locus *ndhF* that is monomorphic in *T. monococcum*. Splits separating the α and β races from γ are highlighted in red and blue, respectively. The position of *T.m.m.* accession 314 groups stably within the β /M race in (A), but lies outside the split uniting race β because it carries a rare allele (haplotype X) at the *pinB* locus that is otherwise characteristic for the race α (see also fig. 5E).

Table 1. Overview of haplotypes found at 18 loci among 452 lines sequenced

Locus	Exon ^(a)	Intron ^(a)	SNPs in			N ^(e)	No. of genotype-specific haplotypes					
			Ex ^(b)	In ^(c)	Indels ^(d)		α	γ	β	M	ae	U
<i>BAMY1</i>	255	214	4	9	2 (10)	11	1	3				3
<i>GAPDH</i>	300	261	0	3	0 (0)	4	1					1
<i>ACC1</i>	411	393	2	5	4 (55)	7	2	1				1
<i>PGK1</i>	441	275	6	15	1 (9)	5			2			2
<i>AGPL</i>	454	555	16	48	9 (15)	15	4	3	2	1		4
<i>CesA</i>	554	215	2	1	0 (0)	4			1			3
<i>6SFT</i>	87	787	1	34	5 (51)	18	6	3	1	1	1	2
<i>BADH</i>	177	369	6	21	3 (16)	5		2	1			4
<i>PEPC</i>	446	348	1	0	0 (0)	2		1				1
<i>G6PDH</i>	387	362	0	1	1 (1)	3						1
<i>GPT</i>	593	80	1	0	0 (0)	2		1				2
<i>pinB</i>	436	162 ^(g)	11	4	0 (0)	12				1		1
<i>ndhF^(f)</i>	719	0	0	0	0 (0)	1						1
<i>GPX</i>	308	356	7	7	2 (4)	7	1	1				2
<i>Lr10^(h)</i>	0	709	0	23	3 (21)	11	1	1		1		3
<i>RGA2</i>	600	0	41	0	0 (0)	16	2	2		1		1
<i>Q</i>	228	688	0	12	3 (5)	9	2	1				4
<i>VRN1</i>	189	432	3	2	2 (7)	9	2		3			1
TOTAL	6585	6206	101	185	35 (194)	141	23	18	10	5	1	37

^a – number of nucleotide positions in exons and introns in the alignment of 452 lines including *T. urartu*

^b – single nucleotide differences within the exon regions only, excluding *T. urartu*

^c – single nucleotide differences within the intron regions only, excluding *T. urartu*

^d – number of insertions/deletions with number of bp involved in parentheses

^e – number of einkorn haplotypes, gapped sites considered but excluding haplotypes specific to *T. urartu*

^f – chloroplast locus

^g – 5' UTR region rather than intron

^h – The *Lr10* locus is empty in over 296 lines sampled

arisen mutations at ancestrally monomorphic alleles. By contrast, the α, β, and γ einkorn races are distinct by virtue of unique haplotype combinations.

The wild sister of domesticate einkorn

The relationship between *T.m.b.* race β and domesticate einkorn is important for understanding einkorn domestication. In principle, there are three possibilities among which to discriminate: a sister-group relationship, a β-progenitor/*T.m.m.*-descendant relationship, and a *T.m.m.*-progenitor/β-descendant relationship (in which case β could potentially constitute a feral form). In the AFLP and multilocus genotype networks, *T.m.m.* clusters adjacent to, but not within wild race β (fig. 2). This suggests a sister-group relationship, consistent with the finding that five haplotypes are specific to domesticate einkorn, while no haplotypes are uniquely shared by race β and *T.m.m.* (table 1). In a β-progenitor/*T.m.m.*-descendant relationship, *T.m.m.* should cluster within race β, both in AFLP analyses and at the level of haplotypes; were race β a feral form of domesticate einkorn, then the former should cluster within the latter, as is observed in the case of the known feral form, *T.m.ae.* (fig. 2). But neither of those patterns is observed. Furthermore, despite extensive sampling of wild habitats, race β was so far found only in the Karacadag (KK) and Kartal-Karadag

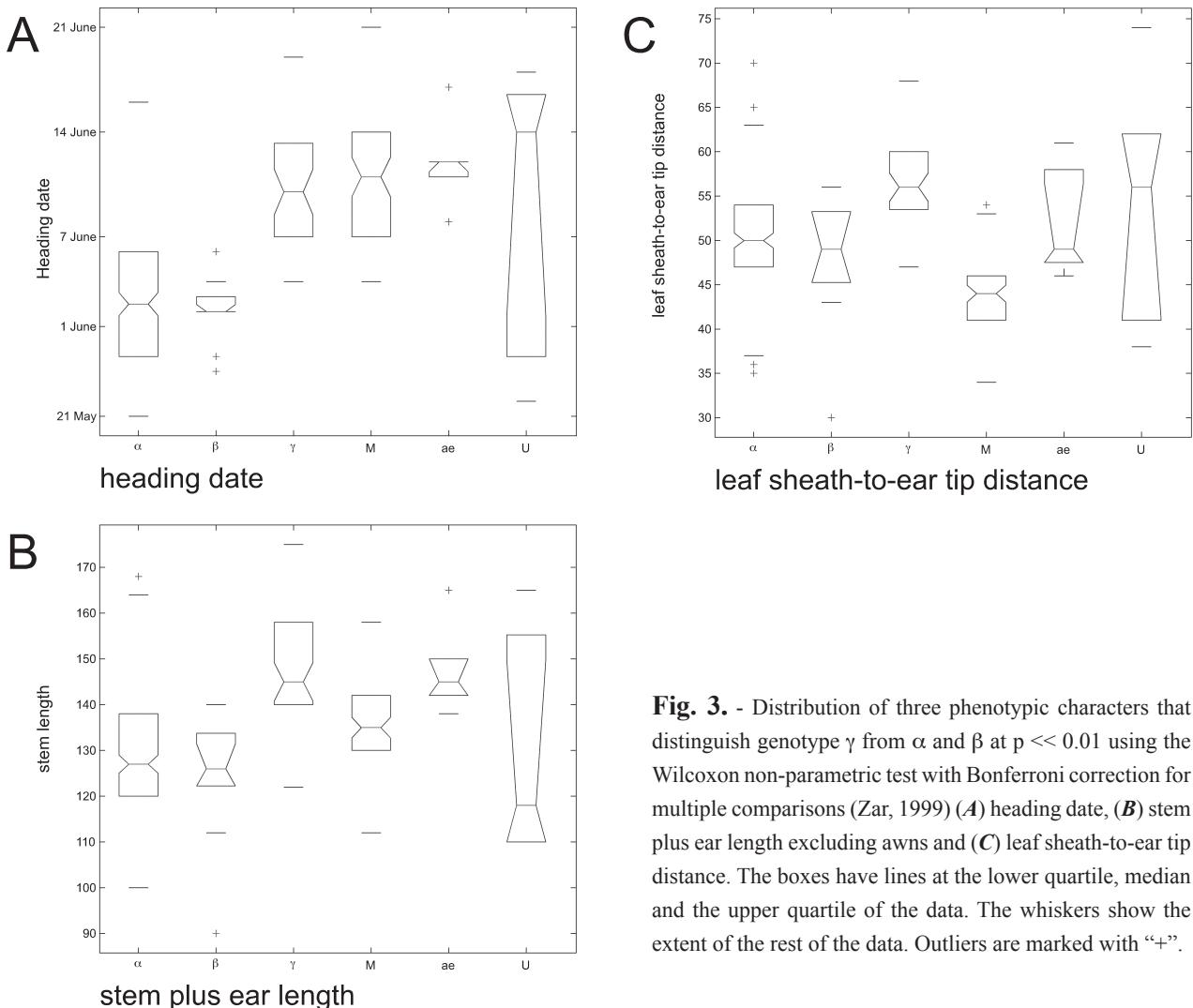


Fig. 3. - Distribution of three phenotypic characters that distinguish genotype γ from α and β at $p << 0.01$ using the Wilcoxon non-parametric test with Bonferroni correction for multiple comparisons (Zar, 1999) (A) heading date, (B) stem plus ear length excluding awns and (C) leaf sheath-to-ear tip distance. The boxes have lines at the lower quartile, median and the upper quartile of the data. The whiskers show the extent of the rest of the data. Outliers are marked with “+”.

(KT) mountain ranges (fig. 1), a region within or at the border of the ‘core area’ defined by Lev-Yadun et al. (2000) in the upper part of the Tigris-Euphrates valleys. The absence of *T.m.ae.*-like lines in the KK and KT regions, the distinctly wild phenotype of race β (as opposed to the recognizably feral phenotype of *T.m.ae.*), the sister relationship of race β and domesticated forms in fig. 2, and the presence of 10 haplotypes specific to race β (table 1), together indicate that race β is not a feral form of *T.m.m.*, and not the direct progenitor of *T.m.m.* Rather, the wild race β is the sister of domesticate einkorn. It currently possesses a very restricted dispersal range within the KK and KT regions (fig. 1), which are characterized by basaltic soils — a habitat factor that might figure into einkorn domestication, given that wild *T. urartu* is known to prefer basaltic soils (Zohary and Hopf 2000).

No reduction of genetic diversity in domesticate einkorn

Previous studies of crop domestication among various species have reported evidence for reduction of genetic diversity attributed to domestication (domestication bottlenecks) (Buckler et al. 2001; Wright et al. 2005; Doebley et al. 2006). Although we do observe a bottleneck-effect in the wild *T. urartu* outgroup, we find no reduction of genetic diversity in domesticate einkorn. On the contrary, nucleotide diversity within *T.m.m.* is greater than within its wild sister, race β . Across the 17 nuclear loci present in nearly all lines sampled — excluding *Lr10*, which is an empty locus in 296 lines (Isidore et al. 2005) — silent site nucleotide diversity, π , varies in a locus-dependent, rather than in a race- or lineage dependent manner (fig. 4). Using

Table 2. Haplotype and nucleotide diversity in wild and domesticate lines

species/ssp/race	n ^(a)	H ^(b)	Hd ^(c)	$\pi_{tot}^{(d)}$	$\pi_{sil}^{(d)}$	$\theta_{tot}^{(d)}$	$\theta_{sil}^{(d)}$
<i>T.m. boeoticum</i>	321	114	0.380	4.73	8.51	3.45	4.29
<i>T.m.b.-α</i>	230	77	0.242	3.48	6.37	2.72	3.23
<i>T.m.b.-γ</i>	49	75	0.362	4.59	7.81	4.20	5.27
<i>T.m.b.-β</i>	42	43	0.260	1.56	2.70	2.05	2.15
<i>T.m. monococcum (M)</i>	84	61	0.278	2.97	5.44	2.45	2.89
<i>T.m. aegilopoides (ae)</i>	8	35	0.353	3.75	6.35	3.45	3.42
<i>T. urartu (U)</i>	39	35	0.276	0.53	0.92	0.66	0.96

^a – Number of lines^b – Number of haplotypes found (gapped sites and the *Lr10* locus excluded)^c – Nei's unbiased estimate of haplotype diversity for inbreeding species (Nei 1987)^d – Values of nucleotide diversity Pi (π) and Waterson's estimator (θ) are given ·10³

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.

the Friedman non-parametric test (Friedman 1937) for comparison of medians while accounting for locus-dependency, the distributions of π for wild races and domesticate einkorn are not different ($P=0.129$). There is thus no significant reduction of polymorphism in domesticated einkorn in comparison to its wild relatives, including race β . The same is reflected at the level of haplotype diversity detected (table 2). Nucleotide diversity across loci (π_{tot}) also uncovers no reduction of diversity, because π_{tot} in domesticate einkorn is higher than that in race β (table 2), but π_{tot} primarily reflects π at the most polymorphic loci only.

We calculated the loss of diversity, $L_\pi = 1 - (\pi_{domest}/\pi_{wild})$ (Tenaillon et al. 2004), at individual loci for domesticate vs. wild einkorn accessions (and *T. urartu* for comparison), the results (table 3) show the lack of diversity loss in domesticate einkorn. In the comparison of *T.m.m.* to *T.m.b.* race β , π underwent no reduction during domestication. Rather, it is higher in *T.m.m.* than in the wild sister at ten of the 18 loci sampled (indicated by negative values of L_π in table 3). At only two loci (*PGK1* and *VRNI*) is a reduction of π in *T.m.m.* observed in comparison to all three wild races, but in both cases owing to a monomorphic *T.m.m.* locus. By

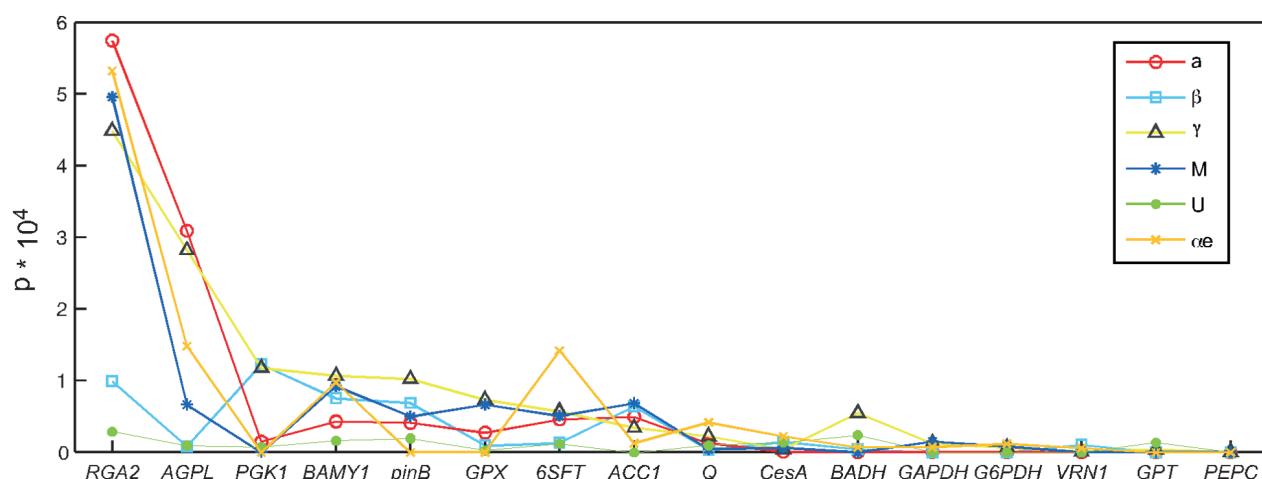


Fig. 4. – Nucleotide diversity at silent sites across sampled loci (except *Lr10*) from *T.m.b.* α, β, and γ races, *T.m.ae.*, *T.m.m.* and *T. urartu*. Taxon designations as in fig. 1 and fig. 2. Note the low diversity in *T. urartu* (U), and lack thereof in domesticate einkorn (M).

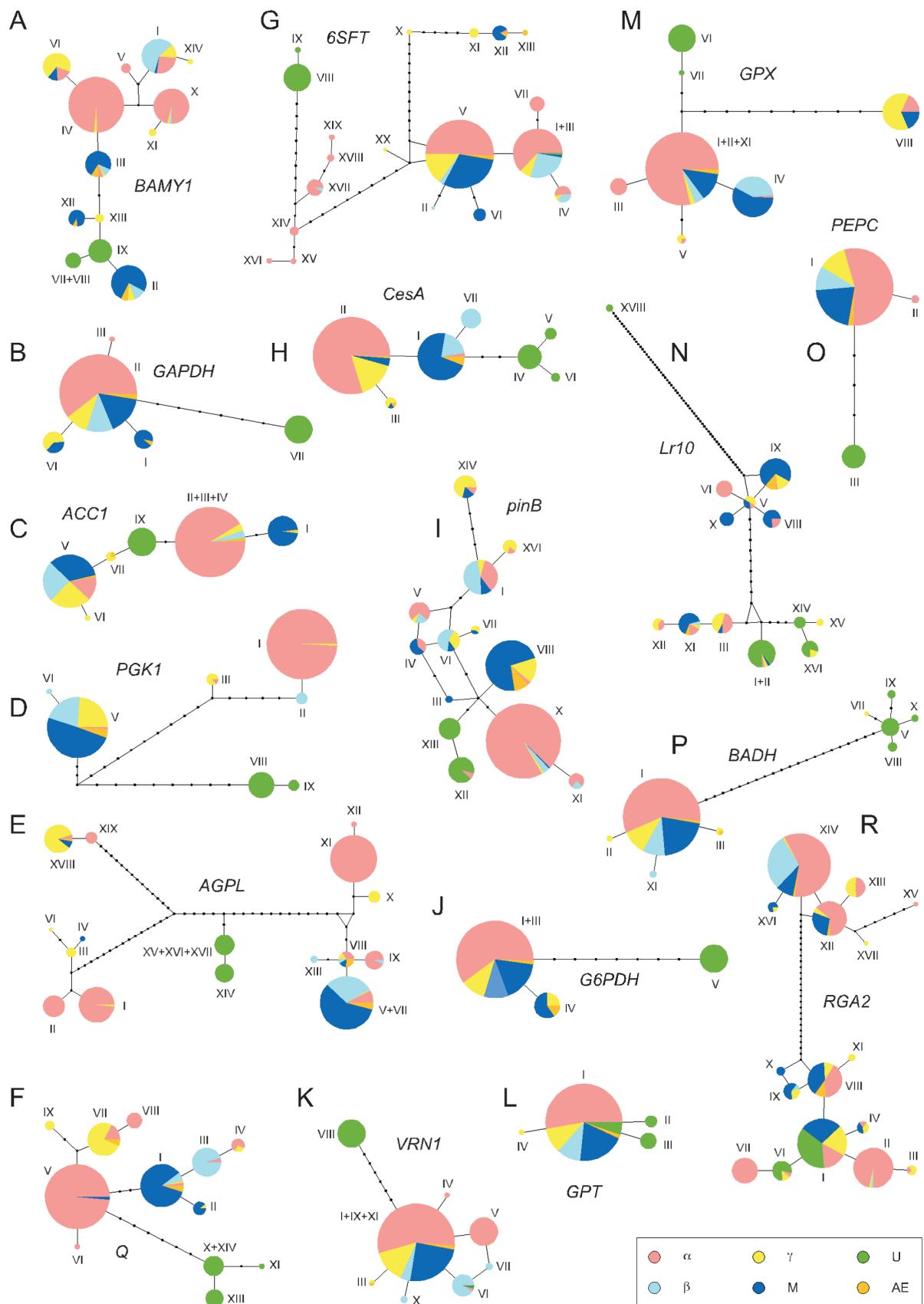


Fig. 5. - Median Joining (MJ) networks for 17 loci except the chloroplast locus *ndhF* where only two haplotypes among all lines were found (monomorphic for all *T. monococcum* lines and one other haplotype in all *T. urartu* lines). Haplotypes differing in indel polymorphisms only were grouped together in this analysis such that one haplotype can be designated by more than one Roman numeral. **A**-*BAMY1*, **B**-*GAPDH*, **C**-*ACC1*, **D**-*PGK1*, **E**-*AGPL*, **F**-*Q*, **G**-*6SFT*, **H**-*CesA*, **I**-*pinB*, **J**-*G6PDH*, **K**-*VRN1*, **L**-*GPT*, **M**-*GPX*, **N**-*Lr10*, **O**-*PEPC*, **P**-*BADH*, **R**-*RGA2*.

Table 3. Changes in nucleotide diversity per locus among wild and domesticate lines

Locus	Loss of diversity ^(a) [in %] in comparisons					Races with $\pi_{\text{tot}} = 0^{\text{(c)}}$		
	M/α	M/γ	M/β	M/boe ^(b)	U/boe	β	U	
<i>BAMY1</i>	-85 ^(d)	11	-27	-40	79			
<i>GAPDH</i>	-2833	-17	-*	-42	100	β	U	
<i>ACCI</i>	-441	-101	-135	-84	100		U	
<i>PGK1</i>	100	100	100	100	96	M		
<i>AGPL</i>	79	77	-706	80	97			
<i>CesA</i>	-933	-55	54	38	-28			
<i>6SFT</i>	-9	12	-217	-11	74			
<i>BADH</i>	0*	100	100	100	-162	α	M	
<i>PEPC</i>	100	0*	0*	*	100	γ	M	U
<i>G6PDH</i>	-*	-21	-*	-571	100	α	β	U
<i>GPT</i>	0*	100	0*	100	-5550	α	β	M
<i>pinB</i>	-35	62	28	31	78			
<i>ndhF</i>	0*	0*	0*	0*	0*	α	β	M
<i>GPX</i>	-142	9	-606	9	97			
<i>Lr10^(e)</i>	25	33	-*	30	-22	β		
<i>RGA2</i>	9	-10	-407	9	97			
<i>Q</i>	62	79	-48	84	66			
<i>VRNI</i>	100	100	100	100	100	M	U	

^a – Loss of diversity was calculated as $L_\pi = 1 - (\pi_{\text{domest}}/\pi_{\text{wild}})$ (Tenaillon et al. 2004) for the wild races indicated with gapped positions excluded.

^b – All wild *T.m. boeticum* accessions ($\alpha + \gamma + \beta$) were pooled for calculation of π_{wild} .

^c – L_π could not be calculated when the wild accessions were monomorphic for the locus ($\pi = 0$) as indicated by an asterisk (*). The value -* indicates that the wild race was monomorphic but domesticate was not, hence higher diversity exists in the domesticate form. The value 0* indicates that both wild and domesticate were monomorphic at the locus, hence no loss of diversity is observed, even though L_π could not be calculated. Races monomorphic for the locus are shown in the right-hand columns.

^d – negative values result when π is greater in domesticate than in wild accessions

^e – The *Lr10* locus is empty in over 296 accessions sampled here.

comparison, four, two, and six loci are monomorphic among the α, γ, and β races, respectively. In 31/54 comparisons of *T.m.b.* races to *T.m.m.*, either no loss of diversity or an increase in *T.m.m.* is observed.

Had we mistakenly grouped the α, β, and γ races together as a single uniform *T.m.b.* “boe” gene pool for the calculation of diversity loss, we might have gained the impression that a loss of diversity had been occurred at some loci during domestication (table 3). But through sampling hundreds, rather than dozens, of wild lines, the data reveal that einkorn domestication did not involve random sampling of wild diversity, rather it entailed a specific and naturally-preexisting race instead. Table 4 summarizes several previous studies of plant domestication where evidence for domestication bottlenecks was reported, but in most cases, comparatively few wild lines were investigated, with rice (Londo et al. 2006) being a notable exception. It remains to be seen whether larger wild samples of other crop species might uncover similar levels of unexpected natural genetic differentiation as is found for einkorn. Similarly, it remains to be seen whether continued sampling of lines and loci in einkorn confirm the present trends, in particular with respect to the high diversity of race γ and the narrow geographical distribution of race β.

In einkorn we observe low diversity in some loci relative to others, but that reduction is found both in the wild races and in domesticated forms. The data for 452 lines uncover no loci that are significantly

Table 4. Selected studies reporting evidence for diversity loss during domesticated plants (based on sequence informations)

	Wild	n _{wild}	Domesticated	n _{dom}	Loci	bp	reference
Fabaceae							
alfalfa	<i>Medicago sativa</i> ssp. <i>sativa</i>	19	<i>Medicago sativa</i> ssp. <i>sativa</i>	31	2	60.500	Muller et al. 2006
soybean	<i>Glycine soja</i>	26	<i>Glycine max</i>	94	102	~6.300.000	Hyten et al. 2006
Asteraceae							
sunflower	<i>Helianthus annuus</i>	16	<i>Helianthus annuus</i>	16	9	262.624	Liu and Burke 2006
Poaceae							
rice	<i>Oryza rufipogon/O. nivara</i>	161*	<i>O. sativa</i>	203*	3	1.636.040	Londo et al. 2006
		30		30	10	484.740	Zhu et al. 2007
pearl millet	<i>Oryza rufipogon</i> and 5 other AA species	44	<i>O. sativa/O. glaberrima</i>	275	3	675961	Kawakami et al. 2007
sorghum	<i>Pennisetum glaucum</i>	6	<i>Pennisetum glaucum</i>	10	1	31.760	Gaut and Glegg 1993
maize	<i>Sorghum bicolor</i> ssp. <i>verticilliflorum</i>	3	<i>S. bicolor</i> ssp. <i>bicolor</i>	24	95	788.022	Hamblin et al. 2006
	<i>Zea mays</i> ssp. <i>mays</i>	16		25	12	358.007	Tenaillon et al. 2004
barley	<i>Hordeum spontaneum</i>	14	<i>Hordeum vulgare</i>	14	774	~6.400.000	Wright et al. 2005
		8		16	23	65.328	Russell et al. 2004
		25		20	7	252.720	Kilian et al. 2006
wheat	<i>Triticum dicoccoides</i>	34		97	5	936.650	Caldwell et al. 2006
	<i>Triticum boeoticum/T. urartu</i>	25+		32	7	624.820	Morrell and Clegg 2007
		28	<i>Triticum dicoccum</i>	12	21	868.800	Haudry et al. 2007
		360	<i>T.m.monococcum/T.m.aegilopoides</i>	92	18	~12.000.000	This study**

bp estimated amount of base pairs (bp) sequenced
Loci Number of loci investigated

n_{wild} Number of wild lines studied
n_{dom} Number of domesticate lines studied

* populations, different numbers of individuals studied per locus
+ three loci with additional wild lines sequenced
** no domestication bottleneck found

more polymorphic in wild than in domesticate lines. Because the monomorphic loci of domesticates are often monomorphic in the wild lines as well (fig. 4; table 3), there is no observed reduction of diversity at any locus that could readily be attributed to the domestication process. The only evidence that we see for a loss of diversity in the present data is in the outgroup, *T. urartu* (fig. 4; table 3).

It remains possible that selection underlies some differences in polymorphisms that we observe across loci, but if so, then the same selection is operating in both wild and domesticate populations and can thus hardly be ascribed to domestication, even for loci such as *Lr10* or *Q* that are known to be important for modern breeding (Salamini et al. 2002; Isidore et al. 2005). We clearly see evidence for recombination in the present data because we find a low frequency of heterozygous loci among otherwise homozygous individuals. With the exception of the feral form *T.m.ae.*, we did not observe any obvious hybrids of wild and domesticate einkorn, although wild and domesticate einkorn are interfertile (Zohary and Hopf 2000) and the existence of some introgression cannot be excluded, for example, in the case of the otherwise race α -specific *pinB* locus in domesticate accession number 314 (see legend to fig. 2).

The present findings appear to be unique among haplotype-based investigations of crop domestication genetics to date in two respects. First, a natural race, *T.m.b.* β , has been identified both by haplotype and AFLP data that is genetically more similar to the domesticate form than other naturally existing races of the wild species are. Second, einkorn is one of the few domesticate crop species investigated to date that escaped breeding bottlenecks during the green revolution. Notably, there are other examples known of domesticate plants for which no reduction in genetic diversity in the comparison of wild and domesticate forms was found, including chicory (Van Cutsem et al. 2003), bell pepper (Hernandez-Verdugo et al. 2001) and pepino (Blanca et al. 2007). Inferences about domestication bottlenecks from investigation of intensely bred domesticate germplasm (Salamini et al. 2004; Ozkan et al. 2005; Willcox, 2005; Abbo et al. 2006; Doebley et al. 2006; Zhu et al. 2007) are best considered in this light, prompting the following brief reconsideration of current views on einkorn domestication in the Fertile Crescent, based upon archaeological and genetic data.

A dispersed-specific model of einkorn domestication

Over the last decade, a consensus has been reached on the existence of a core area of agricultural development in south-eastern Turkey (Nesbitt and Samuel 1996; Lev-Yadun et al. 2000; Bar-Yosef 2002; Schmidt 2006; Licher 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). Similar wild populations were necessarily the starting material at the origin of agriculture in the Fertile Crescent. Detailed archaeological reports by Hillman (2000) and Willcox (2005) and the newer report of Weiss et al. (2006) describe how the pre-domestication cultivation of (wild) cereals lasted even for centuries in the region, and how it was followed by gradual (Kislev 2002) and multiple (Gebel 2004) appearance of domesticate phenotypes. The genetic and cultural mechanisms underlying the origin of those phenotypes are the issue (Diamond and Belwood 2003).

If geographically distinct domestication events each entailed random sampling from local genotypes, domesticate lines should trace to different localities across the range of the wild progenitor (Jones 2004). This is not observed for einkorn: race β is the sister to domesticate einkorn, but there is no evident reduction of genetic variation. This can be accommodated by a domestication model that we designate as dispersed-specific (fig. 6). In essence, this would entail scenario in which a sedentary natufian society (Bar-Yosef 2002) first harvested, then cultivated the wild β race of *T.m.b.* in the core area, but in a later phase of agricultural expansion, the β race was transferred to other locations, possibly in a process of nascent domestication. Transport could have involved migrating farmers (Nadel 2002; Renfrew 2002) or exchange of seeds against

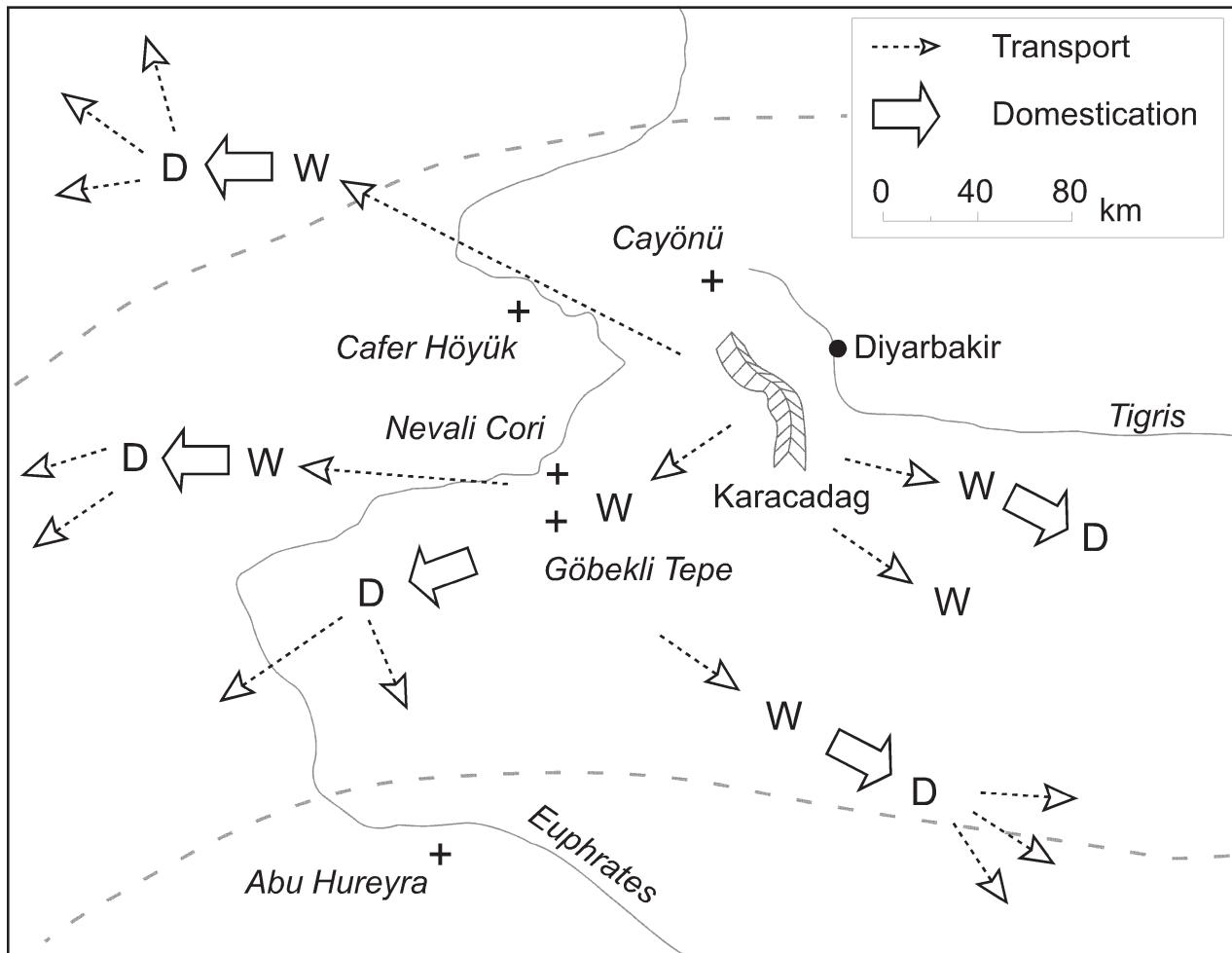


Fig. 6. - The dispersed-specific model for einkorn domestication. Only the Karacadag area in present day Southeast Turkey is shown here. Archaeological sites are indicated in italic. The Fertile Crescent is indicated with a dotted line. W-wild einkorn; D-domesticated einkorn. Note that domestication experiments were not always successful. Topography and environmental conditions determined cereal transport directions. See text for further explanations.

other goods, as not all soils of the Fertile Crescent were adapted to cereal cultivation (Willcox 2005). Given the evidence that wild cereal seeds were harvested at the Ohalo camp (in the Palestine corridor) 21,000 years ago (Nadel 2002), it follows that cereal seeds, particularly hulled forms (Nesbitt and Samuel 1996), were produced and moved across the Fertile Crescent (Willcox 2005). Weedy cereals grown on cultivated fields increased at Abu Hureyra starting about 11,200 years ago (Hillman 2000). Gradually, in several areas, variants of the β race emerged with common domesticated traits.

Across cereal species, domestication was unquestionably a convergent genetic event: the same genes for the same traits underlie domestication in different crops (Salamini et al. 2002; Pozzi et al. 2004). Thus, the sequestering of the same traits and genes independently within a given crop can have posed no more of a technological barrier than the same feat across different crops. Through spread of a common technology, domesticate lines could have emerged independently in different places from local samples of the β race. In this process, a genetic bottleneck would have occurred at each domesticating human settlement, but domestication events at numerous villages would have allowed the newly domesticated lines to integrate a full arsenal of wild haplotypes: many independent domestication bottlenecks would result in no domestication bottleneck for the domesticate lines as a whole.

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

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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, as also new archaeological data underscore (Weiss et al. 2006; Licher 2007).

Although the einkorn β race is so far only found in the KK and KT mountains, it might have been more widely dispersed throughout the Fertile Crescent and southeast Turkey 12,000 years ago, such that KK and KT harbour only relic populations. While still consistent with our dispersed-specific model, that would allow the possibility that only domestication technology, not race β seeds, was exported from the core area. Finally, it has been proposed that harvesting wild seeds with a basket (Harlan 1989) accumulates disarticulating wild spikelets, while mutant plants with stiff rachis will not be harvested, such that their mutant frequency will increase in a given field with time (Hillman and Davies 1990). Unintentional selection, accompanied by repeated sowings of wild material, might have thus increased rachis stiffness and seed size, thereby completing the domestication process for einkorn.

Supplementary Information

Supplementary material mentioned in the text, comprising 5 supplementary tables are available at *Molecular Biology and Evolution* online (<http://www.mbe.oxfordjournals.org>). Sequence data from this article are deposited in GenBank Data library under accession no. provided in Supplementary table S5.

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Supplementary Material

I. Supplementary Tables

Supplementary Table S1. Details and collection sites for 603 lines used for figure 2*A*

Supplementary Table S2. Details and collection sites for 452 lines that were sequenced for 18 loci, used for figure 2*B*

Supplementary Table S3. Loci, sequence-source, chromosomal position, and function

Supplementary Table S4. Primer and PCR conditions

Supplementary Table S5. GenBank accession numbers for einkorn haplotypes

II. Supplementary References

Supplementary Table S1. Details and collection sites for 603 lines used for figure 2A. Lines designated with an asterisk were used for haplotype studies

ID-N°	Race	Accession	Name	Source	Origin	Alt	Lat	Long
4*	M	PI 94740	<i>T. monococcum</i>	Can/A	Spain, Valki Exp. Station	40'00"	40'00"	04'00"
5*	M	PI 119435	<i>T. monococcum</i>	Can/A	Turkey, Balkesir, Okcugeli	41'12"	36'11"	36'10"
7*	M	PI 167615	<i>T. monococcum</i>	Can/A	Turkey, Balkesir, seed store in Bandirma	40'03"	40'20"	27'58"
8*	M	PI 167625	<i>T. monococcum</i>	Can/A	Turkey, Ankara, Yenisehir	39'55"	32'52"	25'00"
14*	M	PI 254195	<i>T. monococcum</i>	Can/A	Greece, Crete, Mesava Plain Exp. Station	35'02"	25'00"	44'12"
15*	M	PI 264935	<i>T. monococcum</i>	Can/A	Romania, Botanical Garden?	46'00"	36'24"	
26*	M	PGR 10805	<i>T. boeoticum</i>	Can/A	Iraq, Arbil, 1 km NE of Salahadin	1100		
49*	α	PGR 6150	<i>T. boeoticum</i>	Can/A				
68	M	G 4325	<i>T. monococcum sinistrale</i>	Can/A	originally from Turkey			
69*	M	TRI 612/74 SKL	<i>T. monococcum</i> var. <i>softianum</i>	IPK	Albania, Kelyra, Vjossa valley			
102*	M	TRI 618/74 SKL	<i>T. monococcum</i> var. <i>vulgare</i>	IPK	Albania, Kelyra, Vjossa valley			
104*	M	AT 12910/89	<i>T. monococcum vulgare</i>	IPK	Albania, Prens			
109*	M	BGRC 3521	<i>T. monococcum erodiumium</i>	BGRC	Hungary?			
115*	M	BGRC 7038	<i>T. monococcum vulgare</i>	BGRC	originally from Turkey			
120*	M	TRI 11525/76 SKL	<i>T. monococcum sinistrale</i> <i>flata</i>	IPK				
122	U	HRI 673/583	<i>T. urartu</i>	IPK	Armenia			
123*	ae	A Schegl/88	<i>T. boeoticum rufinigrum</i>	IPK	Azerbaijan			
126	γ	TRI 6734/89	<i>T. boeoticum</i> (ex. <i>T. urartu</i>)	IPK	originally from Turkey			
127*	M	TRI 1990/74 SKL	<i>T. monococcum sinistrale</i>	BGRC	Albania, Kelyra, Vjossa valley			
137*	M	BGRC 13182	<i>T. monococcum erodiumium</i>	BGRC	ODR			
152*	M	BGRC 13187	<i>T. monococcum horrenmannii</i>	BGRC	Italy			
187*	M	BGRC 13187	<i>T. monococcum vulgare</i>	BGRC	Balkans			
189*	M	BGRC 13189	<i>T. monococcum softianum</i>	BGRC	Balkans			
190*	M	BGRC 13193	<i>T. monococcum nigricutatum</i>	BGRC	Austria, Vorarlberg			
194*	M	BGRC 13196	<i>T. monococcum horrenmannii</i>	BGRC	Austria, Vorarlberg			
197*	M	BGRC 20451	<i>T. monococcum nigricutatum</i>	BGRC	Balkans			
209*	M	BGRC 20518	<i>T. boeoticum larionovi</i>	BGRC	Balkans			
210*	ae	BGRC 20521	<i>T. monococcum pseudoflavescens</i>	BGRC	Balkans			
211*	M	BGRC 36546	<i>T. boeoticum zuccharini aglospoides</i>	MP1-Cologne	Balkans			
226*	ae	BGRC 36547	<i>T. boeoticum larionovi aglospoides</i>	MP1-Cologne	Balkans			
227*	ae	BGRC 36548	<i>T. monococcum maysuriyan aglospoides</i>	MP1-Cologne	Balkans			
228*	ae	BGRC 36551	<i>T. boeoticum maysuriyan aglospoides</i>	MP1-Cologne	Balkans			
229*	γ	BGRC 36556	<i>T. monococcum latissimum</i>	MP1-Cologne	Bulgaria			
233*	M	BGRC 37351	<i>T. monococcum albohorrenmannii</i>	MP1-Cologne	Germany			
259*	M	BGRC 42006	<i>T. monococcum vulgare</i>	MP1-Cologne	Sweden			
269*	M	BGRC C-2016	<i>T. monococcum nigricutatum</i>	MP1-Cologne	Balkans			
279*	M	BGRC C-2017	<i>T. monococcum macedonicum</i>	MP1-Cologne	Albania, Kelyra, Vjossa valley			
280*	M	BGRC C-2019	<i>T. monococcum horrenmannii</i>	MP1-Cologne	Spain			
282*	M	BGRC 43448	<i>T. monococcum flavescens</i>	MP1-Cologne	France			
303*	M	BGRC 43451	<i>T. monococcum macedonicum</i>	MP1-Cologne	Balkans			
306*	M	BGRC 43454	<i>T. monococcum horrenmannii</i>	MP1-Cologne	Germany			
309*	M	BGRC 43456	<i>T. monococcum horrenmannii</i>	MP1-Cologne	Syria			
311*	M	BGRC 43459	<i>T. monococcum horrenmannii</i>	MP1-Cologne	Balkans			
314*	M	BGRC 43466	<i>T. monococcum macedonicum</i>	MP1-Cologne	Lebanon, El Beqaia, between Kfarkouk and Aiba			
320*	M	BGRC 43466	<i>T. monococcum horrenmannii</i>	MP1-Cologne	USA/KS			
328*	M	BGRC 43474	<i>T. monococcum flavescens</i>	MP1-Cologne	USA/KS	33'31"	33'31"	39'41"
351*	M	BGRC 43497	<i>T. monococcum horrenmannii</i>	MP1-Cologne	USA/KS	37'14"	37'14"	
353*	M	BGRC 43499	<i>T. monococcum horrenmannii</i>	MP1-Cologne	USA/KS	33'56"	33'56"	36'06"
355*	M	BGRC 43501	<i>T. monococcum horrenmannii</i>	MP1-Cologne	USA/KS	34'04"	34'04"	46'29"
379*	α	198	<i>T. monococcum boeoticum</i>	MP1-Cologne	USA/KS	40'30"	40'30"	45'00"
386*	α	747	<i>T. boeoticum</i>	MP1-Cologne	USA/KS			
388*	U	787	<i>T. urartu</i>	MP1-Cologne	USA/KS			
393*	U	831	<i>T. urartu</i>	MP1-Cologne	USA/KS			
394*	U	851	<i>T. urartu</i>	MP1-Cologne	USA/KS			
396*	M	2701	<i>T. monococcum</i>	MP1-Cologne	USA/KS			
409		16273	<i>T. monococcum boeoticum</i>	MP1-Cologne	USA/KS			
432*	M	19842	<i>T. monococcum sofianum</i>	MP1-Cologne	USA/KS			
433*	M	19846	<i>T. monococcum flavescens</i>	MP1-Cologne	USA/KS			
435*	M	19852	<i>T. monococcum sinistrale</i>	MP1-Cologne	USA/KS			
476*	M	90451	<i>T. monococcum var. macedonicum</i>	MP1-Cologne	USA/KS			

CHAPTER 7

ID-N°	Race	Accession	Name	Source	Origin	Alt	Lat	Long
736*	α	PI 427604	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 62 to 71.9 km E of Urfa	662	37°14'	39°23'
741*	α	PI 427609	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 62 to 71.9 km E of Urfa	662	37°14'	39°23'
746*	α	PI 427614	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 16 km E of Siverek	1050	37°43'	39°28'
751*	β	PI 427619	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 16 km E of Siverek	1050	37°43'	39°28'
752*	β	PI 427620	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20.2 km E of Siverek	1200	37°43'	39°30'
753*	α	PI 427621	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakir, 52.5 km W of Diyarbakir in the Karacadag	1400	37°47'	39°46'
754*	β	PI 427622	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakir, 52.5 km W of Diyarbakir in the Karacadag	1400	37°47'	39°46'
755	β	PI 427624	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakir, 52.5 km W of Diyarbakir in the Karacadag	1400	37°47'	39°46'
757*	β	PI 427626	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakir, 52.5 km W of Diyarbakir in the Karacadag	1400	37°47'	39°46'
758*	β	PI 427627	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakir, 52.5 km W of Diyarbakir in the Karacadag	1400	37°47'	39°46'
760*	β	PI 427629	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20.2 km E of Siverek	1200	37°43'	39°30'
763*	β	PI 427632	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20.2 km E of Siverek	1200	37°43'	39°30'
765*	β	PI 427634	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20.2 km E of Siverek	1200	37°43'	39°30'
766*	β	PI 427635	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20.2 km E of Siverek	1200	37°43'	39°30'
767*	β	PI 427636	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20.2 km E of Siverek	1200	37°43'	39°30'
771*	α	PI 427640	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1km NE of Salahadin	1100	36°24'	44°12'
775*	α	PI 427644	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1km NE of Salahadin	1100	36°24'	44°12'
777*	α	PI 427646	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1km NE of Salahadin	1100	36°24'	44°12'
779*	α	PI 427648	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1km NE of Salahadin	1100	36°24'	44°12'
782*	α	PI 427651	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1km NE of Salahadin	1100	36°24'	44°12'
784*	α	PI 427653	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1km NE of Salahadin	1100	36°24'	44°12'
787*	α	PI 427656	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1km NE of Salahadin	1100	36°24'	44°12'
790*	α	PI 427659	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1km NE of Salahadin	1100	36°24'	44°12'
795*	α	PI 427664	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1km NE of Salahadin	1100	36°24'	44°12'
797*	α	PI 427666	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 4 km NE of Sheqlawwa	1000	36°25'	44°22'
800*	α	PI 427669	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 4 km NE of Sheqlawwa	1000	36°25'	44°22'
803*	α	PI 427672	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 4 km NE of Sheqlawwa	1000	36°25'	44°22'
807*	α	PI 427676	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 21 km S of Harr	1000	36°25'	44°22'
815*	α	PI 427684	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 21 km S of Harr	1000	36°25'	44°22'
818*	α	PI 427688	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 21 km W of Sheqlawwa	1000	36°20'	44°11'
821*	α	PI 427691	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Sheqlawwa	1000	36°23'	44°14'
824*	α	PI 427694	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Sheqlawwa	1000	36°23'	44°14'
827*	α	PI 427697	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Sheqlawwa	1000	36°23'	44°14'
830*	α	PI 427700	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Sheqlawwa	1000	36°23'	44°14'
834*	α	PI 427704	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Sheqlawwa	1000	36°23'	44°14'
839*	α	PI 427709	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Sheqlawwa	1000	36°23'	44°14'
840*	α	PI 427710	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, 5.5 km N of Dohuk	750	36°55'	43°02'
843*	α	PI 427713	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, 5.5 km N of Dohuk	750	36°55'	43°02'
862*	α	PI 427733	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, 24 km NE of Dohuk	950	36°58'	43°11'
864*	α	PI 427735	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, 2 km W of Suara Tuka	1250	36°58'	43°11'
868*	α	PI 427739	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, 2 km W of Suara Tuka	1250	36°58'	43°11'
870*	α	PI 427741	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, 6 km E of Suara Tuka	1050	37°00'	43°13'
871*	α	PI 427742	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, 6 km E of Suara Tuka	1050	37°00'	43°13'
875*	α	PI 427747	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, between Zawita and Suara Tuka	1380	36°58'	43°11'
895*	α	PI 427768	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, between Zawita and Suara Tuka	1380	36°58'	43°11'
906*	α	PI 427779	<i>T. boeoticum</i>	USDA	Iraq, As Salaymanyah, 44 km NW of Sulaimaniya	700	35°47'	45°08'
907*	α	PI 427780	<i>T. boeoticum</i>	USDA	Iraq, As Salaymanyah, 25 km E of Sulaimaniya	700	35°47'	45°08'
909*	α	PI 427782	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabadd	960	35°41'	45°29'
910*	α	PI 427783	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabadd	1500	34°04'	46°29'
923*	α	PI 427796	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabadd	1500	34°04'	46°29'
925*	α	PI 427798	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 34 km E of Kamiran	1900	34°50'	47°10'
933*	α	PI 427808	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 9 km NW of Kermanshah	1400	34°23'	47°02'
936*	α	PI 427809	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 36 km NW of Shahabadd	1561	34°17'	46°13'
938*	α	PI 427811	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabadd	1500	34°04'	46°29'
939*	α	PI 427812	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabadd	1500	34°04'	46°29'
941*	α	PI 427814	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabadd	1500	34°04'	46°29'
944*	α	PI 427817	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabadd	1100	36°24'	44°12'
947*	α	PI 427820	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabadd	1100	36°24'	44°12'
953*	α	PI 427826	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabadd	1100	36°24'	44°12'
956*	α	PI 427829	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabadd	1100	36°24'	44°12'
960*	α	PI 427833	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabadd	1100	36°24'	44°12'
963	α	PI 427836	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabadd	1100	36°24'	44°12'

CHAPTER 7

ID-N°	Race	Accession	Name	Source	Origin	Alt	Lat	Long
1139*	M	PI428160	<i>T. monococcum</i>	USDA	Turkey, Manisa, Soma	132	39 10'	27 36'
1140*	M	PI428166	<i>T. monococcum</i>	USDA	Turkey, Bursa, Gürsu	125	40 13'	29 12'
1141*	γ	PI470718	<i>T. boeoticum</i>	USDA	Turkey, Nevşehir, 9 km SE of Urgup	1200	38 36'	35 00'
1142*	γ	PI470722	<i>T. boeoticum</i>	USDA	Turkey, Kayseri, 10 km NE of Pınarbaşı	1510	38 46'	36 29'
1143*	γ	PI470723	<i>T. boeoticum</i>	USDA	Turkey, Kayseri, 46 km NE of Pınarbaşı	1770	38 53'	36 46'
1144*	α	PI470726	<i>T. boeoticum</i>	USDA	Turkey, Elazığ, 25 km SW of Elazığ	1160	38 32'	39 02'
1148*	α	PI503302	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 116 km W of Kızıltepe	800	37 14'	39 23'
1150*	α	PI503304	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 52.5 km NE of Urfa, near Hilvan	650	37 33'	38 55'
1151*	α	PI503305	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahaddin	1100	36 24'	44 12'
1153*	α	PI503307	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, 24 km NW of Dahuk	950	36 58'	43 11'
1156*	α	PI503358	<i>T. boeoticum</i>	USDA	Iran, Bakhtaran, 47 km NW of Shahabad	1500	34 20'	46 08'
1157	M	PI518452	<i>T. monococcum</i>	USDA	Spain, Cadiz, Prado del Rey, Sierra de Cadiz	236	36 47'	05 34'
1161*	α	PI538527	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 80.5 km W of Kızıltepe	670	37 14'	39 43'
1166*	α	PI538532	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 2.9 km S of Viranşehir	600	37 13'	39 47'
1170*	α	PI538536	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 52.5 km NE of Urfa, near Hilvan	650	37 33'	38 55'
1173	β	PI538539	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakır, 52.5 km W of Diyarbakır in the Karacadag	1400	37 47'	39 46'
1174*	β	PI538540	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakır, 52.5 km W of Diyarbakır in the Karacadag	1400	37 47'	39 30'
1175	α	PI538541	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20.2 km E of Siverek	1200	36 24'	44 14'
1179*	α	PI538545	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 2 km NW of Salahaddin	1100	36 24'	44 22'
1181*	α	PI538547	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 4 km NE of Sheqlawaya	1000	36 25'	44 22'
1182*	α	PI538548	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 4 km NE of Sheqlawaya	1000	36 25'	44 22'
1187*	α	PI538553	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Sheqlawaya	1000	36 23'	44 14'
1190*	α	PI538556	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, 5.5 km N of Siverk	750	36 55'	43 02'
1194*	α	PI538560	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, 24 km NW of Dahuk towards Amadiya	950	36 58'	43 11'
1196*	α	PI538562	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 2 km W of Shara Tuka	1250	36 58'	43 11'
1199*	α	PI538565	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, 6 km E of Shara Tuka	1050	37 00'	43 13'
1201*	α	PI538567	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 6 km E of Shara Tuka	1050	37 00'	43 13'
1204*	α	PI538570	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Sheqlawaya	1380	36 58'	43 11'
1207*	α	PI538573	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, between Zawita and Shara Tuka	1380	36 58'	43 11'
1210*	α	PI538576	<i>T. boeoticum</i>	USDA	Iran, Bakhtiaran, 5.5 km N of Bisutun	1350	34 26'	47 26'
1211*	α	PI538577	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 2 km W of Shara Tuka	1350	34 26'	44 12'
1213*	α	PI538579	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Shara Tuka	1100	36 24'	44 12'
1215*	α	PI538581	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 6 km E of Shara Tuka	1100	36 24'	44 12'
1220*	α	PI538586	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 21 km S of Hanir	1000	36 25'	44 22'
1221*	α	PI538587	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 21 km S of Hanir	1000	36 25'	44 22'
1222*	α	PI538588	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Sheqlawaya	1000	36 23'	44 14'
1224*	α	PI538591	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Sheqlawaya	1000	36 23'	44 14'
1228*	α	PI538594	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Sheqlawaya	1000	36 23'	44 14'
1231*	α	PI538597	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Sheqlawaya	1000	36 23'	44 14'
1233	U	PI538599	<i>T. uraritu</i>	USDA	Iraq, Dahuk, 24 km NE Dahuk, towards Amadiya	950	36 58'	43 11'
1235*	α	PI538601	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, 6 km E of Suara Tuka	1050	37 00'	43 13'
1238*	α	PI538604	<i>T. boeoticum</i>	USDA	Iraq, Dahuk, 6 km E of Suara Tuka	1050	37 00'	43 13'
1239*	α	PI538605	<i>T. boeoticum</i>	USDA	Iraq, As Salaymaniyah, 43 km NW of Sulaimaniyah near Surdash	800	35 47'	45 08'
1240*	α	PI538606	<i>T. boeoticum</i>	USDA	Iraq, As Salaymaniyah, 12 km S of Sulaimaniyah	832	35 29'	45 32'
1241*	α	PI538607	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 2.9 km S of Viranshiri	600	37 13'	39 47'
1245*	α	PI538611	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahaddin	1100	36 24'	44 12'
1247*	α	PI538613	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 2 km W of Shara Tuka	1250	36 58'	43 11'
1250*	α	PI538616	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shara Tuka	1000	36 23'	44 14'
1252*	α	PI538619	<i>T. uraritu</i>	USDA	Turkey, Yozgat, 48 km SE of Gaziantep towards Yavuzeli	800	37 11'	35 40'
1256*	γ	PI554480	<i>T. boeoticum</i>	USDA	Turkey, Gaziantep, 1 km S of Arahan village, 25 km N Yavuzeli	550	37 26'	37 41'
1271*	α	PI554487	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakır, 8 km SW of Dicle	950	38 19'	40 00'
1272*	α	PI554488	<i>T. monococcum</i>	USDA	Turkey, Çanakkale, Eceabat	1050	37 43'	39 35'
1273*	α	PI554491	<i>T. boeoticum</i>	USDA	Turkey, Tekirdağ, Malkara	600	37 37'	38 57'
1274*	α	PI554493	<i>T. uraritu</i>	USDA	Turkey, Edirne, Edirne	85	41 40'	26 34'
1277	U	PI554498	<i>T. uraritu</i>	USDA	Turkey, Gaziantep, 19 km N of Gaziantep towards Yavuzeli	700	37 11'	37 28'
1279*	α	PI554503	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakır, At spring, 7 km S of Cinar (S of Diyarbakır)	625	37 13'	40 28'

1280*	<i>T. boeoticum</i>	PI.554504	α	Turkey, Diyarbakir, At spring, 7 km S of Cinar (S of Diyarbakir)	625	37 39'
1281*	<i>T. boeoticum</i>	PI.554505	α	Turkey, Urfa, 20 km SE of Suverk	450	37 37'
1283*	<i>T. boeoticum</i>	PI.554508	α	Turkey, Urfa, 5.5 km NW of Urfa-Diyarbakir road junction	500	38 46'
1289*	<i>T. boeoticum</i>	PI.554521	γ	Turkey, Izmir, 0.5 km E of Aliaga, E edge of village	60	38 48'
1290*	<i>T. boeoticum</i>	PI.554522	γ	Turkey, Canakkale, 7 km NE of Canakkale on route to Lapseki	60	26 59'
1291*	<i>T. boeoticum</i>	PI.554523	γ	Turkey, Bursa, 11 km N of Yenisehir	80	40 11'
1292*	<i>T. boeoticum</i>	PI.554525	γ	Turkey, Cankiri, 8 km E of Ciftes	370	26 28'
1294*	<i>T. boeoticum</i>	PI.554531	γ	Turkey, Cankiri, 19 km S of Cankiri	1000	29 41'
1295*	<i>T. boeoticum</i>	PI.554532	γ	Turkey, Ankara, 12 km NE of Ankara City limit sign	710	40 49'
1296*	<i>T. boeoticum</i>	PI.554533	γ	Turkey, Ankara, 5.5 km E of Ankara City limit sign	900	33 40'
1297*	<i>T. boeoticum</i>	PI.554535	γ	Turkey, Ankara, 40 km SW Ankara, 3.5 km N Haymana, Haymana road	575	40 02'
1299*	<i>T. boeoticum</i>	PI.554537	γ	Turkey, Ankara, 8.5 km N of Haymana station	1100	39 34'
1300*	<i>T. boeoticum</i>	PI.554538	γ	Turkey, Ankara, 8.5 km N of Haymana station	1100	39 36'
1301*	<i>T. boeoticum</i>	PI.554539	γ	Turkey, Ankara, 8.5 km N of Haymana station	1100	39 36'
1302*	<i>T. boeoticum</i>	PI.554540	γ	Turkey, Ankara, 12.5 km N Haymana, Haymana road	820	32 55'
1303*	<i>T. boeoticum</i>	PI.554542	γ	Turkey, Ankara, 25 km S of Golbasi	1450	32 56'
1304*	<i>T. boeoticum</i>	PI.554543	γ	Turkey, Ankara, 32 km W of Konya	1250	32 40'
1305*	<i>T. boeoticum</i>	PI.554544	γ	Turkey, Konya, 27 km NE of Beysehir	1150	37 52'
1306*	<i>T. boeoticum</i>	PI.554545	γ	Turkey, Konya, 6 km SW of Beysehir	1150	37 39'
1307*	<i>T. boeoticum</i>	PI.554546	γ	Turkey, Konya, 5 km N of Beysehir	1125	32 41'
1308*	<i>T. boeoticum</i>	PI.554547	γ	Turkey, Konya, 5 km N of Beysehir	1125	32 42'
1309*	<i>T. boeoticum</i>	PI.554548	γ	Turkey, Konya, 5 km N of Beysehir	1125	32 42'
1310*	<i>T. boeoticum</i>	PI.554549	γ	Turkey, Konya, 5 km N of Beysehir	1125	32 42'
1311*	<i>T. boeoticum</i>	PI.554550	γ	Turkey, Konya, 18 km N of Beysehir	1120	31 43'
1312*	<i>T. boeoticum</i>	PI.554551	γ	Turkey, Isparta, 1.5 km NW of Egirdir	850	31 41'
1313*	<i>T. boeoticum</i>	PI.554552	α	Turkey, Konya, 6 km SW of Beysehir	1125	31 43'
1314*	<i>T. boeoticum</i>	PI.554553	α	Turkey, Konya, 5 km N of Beysehir	1125	31 43'
1315*	<i>T. boeoticum</i>	PI.554554	α	Turkey, Konya, 5 km N of Beysehir	1125	31 43'
1316*	<i>T. boeoticum</i>	PI.554555	γ	Turkey, Konya, 18 km N of Beysehir	1120	31 43'
1317*	<i>T. boeoticum</i>	PI.554556	γ	Turkey, Konya, 6 km SW of Beysehir	850	31 43'
1318*	<i>T. boeoticum</i>	PI.554557	γ	Turkey, Konya, 6 km SW of Beysehir	1125	31 43'
1319*	<i>T. boeoticum</i>	PI.554558	γ	Turkey, Burdur, 11 km NE of Yesilova	1310	29 47'
1320*	<i>T. boeoticum</i>	PI.554559	γ	Turkey, Burdur, 11 km NE of Yesilova	1310	37 36'
1321*	<i>T. boeoticum</i>	PI.554560	γ	Turkey, Burdur, 11 km NE of Yesilova	1310	37 43'
1323*	<i>T. boeoticum</i>	PI.554573	γ	Turkey, Denizli, 32 km S of Denizli junction to Tavas	1230	29 04'
1324*	<i>T. boeoticum</i>	PI.554575	γ	Turkey, Kirsehir, 10 km SE of Ankara-Kirsehir province border	825	33 39'
1326*	<i>T. boeoticum</i>	PI.554562	γ	Turkey, Kirsehir, 12 km NW of Kirsehir	1000	39 15'
1327*	<i>T. boeoticum</i>	PI.554565	γ	Turkey, Kayseri, 12 km W of Binyan	1225	35 46'
1328*	<i>T. boeoticum</i>	PI.554566	γ	Turkey, Kayseri, 6 km NE of Pinarbas	1510	38 45'
1329*	<i>T. boeoticum</i>	PI.554571	α	Turkey, Elazig, 1 km E of Arapkir-Elazig-Malatya jct. toward Elazig	1000	38 48'
1330*	<i>T. boeoticum</i>	PI.554572	α	Turkey, Elazig, 5 km E of Tunelci-Fingol junction	900	39 01'
1331*	<i>T. boeoticum</i>	PI.554573	α	Turkey, Van, 6 km SE of Van	1990	39 28'
1332*	<i>T. boeoticum</i>	PI.554575	γ	Turkey, Hakkari, 21 km SW of Sevdinli	1125	43 23'
1333*	<i>T. boeoticum</i>	PI.554577	γ	Armenia	1080	37 07'
1334*	<i>T. boeoticum</i>	PI.554578	γ	Armenia	1080	44 31'
1335*	<i>T. boeoticum</i>	PI.554579	γ	Armenia	1080	36 03'
1336*	<i>T. boeoticum</i>	PI.554580	γ	Armenia	1080	34 01'
1337*	<i>T. boeoticum</i>	PI.554581	γ	Armenia	1080	36 03'
1338*	<i>T. boeoticum</i>	PI.554582	γ	Armenia	1080	36 03'
1339*	<i>T. boeoticum</i>	PI.554583	γ	Armenia	1080	36 03'
1340*	<i>T. boeoticum</i>	PI.554584	γ	Armenia	1080	36 03'
1341*	<i>T. boeoticum</i>	PI.554585	γ	Armenia	1080	36 03'
1342*	<i>T. boeoticum</i>	PI.554586	γ	Armenia	1080	36 03'
1343*	<i>T. boeoticum</i>	PI.554587	γ	Armenia	1080	36 03'
1344*	<i>T. boeoticum</i>	PI.554588	γ	Armenia	1080	36 03'
1345*	<i>T. boeoticum</i>	PI.554589	γ	Armenia	1080	36 03'
1346*	<i>T. boeoticum</i>	PI.554590	γ	Armenia	1080	36 03'
1347*	<i>T. boeoticum</i>	PI.554591	γ	Armenia	1080	36 03'
1348*	<i>T. boeoticum</i>	PI.554592	γ	Armenia	1080	36 03'
1349*	<i>T. boeoticum</i>	PI.554593	γ	Armenia	1080	36 03'
1350*	<i>T. boeoticum</i>	PI.554594	γ	Armenia	1080	36 03'
1351*	<i>T. boeoticum</i>	PI.554595	γ	Armenia	1080	36 03'
1352*	<i>T. boeoticum</i>	PI.554596	γ	Armenia	1080	36 03'
1353*	<i>T. boeoticum</i>	PI.554597	γ	Armenia	1080	36 03'
1354*	<i>T. boeoticum</i>	PI.554598	γ	Armenia	1080	36 03'
1355*	<i>T. boeoticum</i>	PI.554599	γ	Armenia	1080	36 03'
1356*	<i>T. boeoticum</i>	PI.554600	γ	Armenia	1080	36 03'
1357*	<i>T. boeoticum</i>	PI.554601	γ	Armenia	1080	36 03'
1358*	<i>T. boeoticum</i>	PI.554602	γ	Armenia	1080	36 03'
1359*	<i>T. boeoticum</i>	PI.554603	γ	Armenia	1080	36 03'
1360*	<i>T. boeoticum</i>	PI.554604	γ	Armenia	1080	36 03'
1361*	<i>T. boeoticum</i>	PI.554605	γ	Armenia	1080	36 03'
1362*	<i>T. boeoticum</i>	PI.554606	γ	Armenia	1080	36 03'
1363*	<i>T. boeoticum</i>	PI.554607	γ	Armenia	1080	36 03'
1364*	<i>T. boeoticum</i>	PI.554608	γ	Armenia	1080	36 03'
1365*	<i>T. boeoticum</i>	PI.554609	γ	Armenia	1080	36 03'
1366*	<i>T. boeoticum</i>	PI.554610	γ	Armenia	1080	36 03'
1367*	<i>T. boeoticum</i>	PI.554611	γ	Armenia	1080	36 03'
1368*	<i>T. boeoticum</i>	PI.554612	γ	Armenia	1080	36 03'
1369*	<i>T. boeoticum</i>	PI.554613	γ	Armenia	1080	36 03'
1370*	<i>T. boeoticum</i>	PI.554614	γ	Armenia	1080	36 03'
1371*	<i>T. boeoticum</i>	PI.554615	γ	Armenia	1080	36 03'
1372*	<i>T. boeoticum</i>	PI.554616	γ	Armenia	1080	36 03'
1373*	<i>T. boeoticum</i>	PI.554617	γ	Armenia	1080	36 03'
1374*	<i>T. boeoticum</i>	PI.554618	γ	Armenia	1080	36 03'
1375*	<i>T. boeoticum</i>	PI.554619	γ	Armenia	1080	36 03'
1376*	<i>T. boeoticum</i>	PI.554620	γ	Armenia	1080	36 03'
1377*	<i>T. boeoticum</i>	PI.554621	γ	Armenia	1080	36 03'
1378*	<i>T. boeoticum</i>	PI.554622	γ	Armenia	1080	36 03'
1379*	<i>T. boeoticum</i>	PI.554623	γ	Armenia	1080	36 03'
1380*	<i>T. boeoticum</i>	PI.554624	γ	Armenia	1080	36 03'
1381*	<i>T. boeoticum</i>	PI.554625	γ	Armenia	1080	36 03'
1382*	<i>T. boeoticum</i>	PI.554626	γ	Armenia	1080	36 03'
1383*	<i>T. boeoticum</i>	PI.554627	γ	Armenia	1080	36 03'
1384*	<i>T. boeoticum</i>	PI.554628	γ	Armenia	1080	36 03'
1385*	<i>T. boeoticum</i>	PI.554629	γ	Armenia	1080	36 03'
1386*	<i>T. boeoticum</i>	PI.554630	γ	Armenia	1080	36 03'
1387*	<i>T. boeoticum</i>	PI.554631	γ	Armenia	1080	36 03'
1388*	<i>T. boeoticum</i>	PI.554632	γ	Armenia	1080	36 03'
1389*	<i>T. boeoticum</i>	PI.554633	γ	Armenia	1080	36 03'
1390*	<i>T. boeoticum</i>	PI.554634	γ	Armenia	1080	36 03'
1391*	<i>T. boeoticum</i>	PI.554635	γ	Armenia	1080	36 03'
1392*	<i>T. boeoticum</i>	PI.554636	γ	Armenia	1080	36 03'
1393*	<i>T. boeoticum</i>	PI.554637	γ	Armenia	1080	36 03'
1394*	<i>T. boeoticum</i>	PI.554638	γ	Armenia	1080	36 03'
1395*	<i>T. boeoticum</i>	PI.554639	γ	Armenia	1080	36 03'
1396*	<i>T. boeoticum</i>	PI.554640	γ	Armenia	1080	36 03'
1397*	<i>T. boeoticum</i>	PI.554641	γ	Armenia	1080	36 03'
1398*	<i>T. boeoticum</i>	PI.554642	γ	Armenia	1080	36 03'
1399*	<i>T. boeoticum</i>	PI.554643	γ	Armenia	1080	36 03'
1400*	<i>T. boeoticum</i>	PI.554644	γ	Armenia	1080	36 03'
1401*	<i>T. boeoticum</i>	PI.554645	γ	Armenia	1080	36 03'
1402*	<i>T. boeoticum</i>	PI.554646	γ	Armenia	1080	36 03'
1403*	<i>T. boeoticum</i>	PI.554647	γ	Armenia	1080	36 03'
1404*	<i>T. boeoticum</i>	PI.554648	γ	Armenia	1080	36 03'
1405*	<i>T. boeoticum</i>	PI.554649	γ	Armenia	1080	36 03'
1406*	<i>T. boeoticum</i>	PI.554650	γ	Armenia	1080	36 03'
1407*	<i>T. boeoticum</i>	PI.554651	γ	Armenia	1080	36 03'
1408*	<i>T. boeoticum</i>	PI.554652	γ	Armenia	1080	36 03'
1409*	<i>T. boeoticum</i>	PI.554653	γ	Armenia	1080	36 03'
1410*	<i>T. boeoticum</i>	PI.554654	γ	Armenia	1080	36 03'
1411*	<i>T. boeoticum</i>	PI.554655	γ	Armenia	1080	36 03'
1412*	<i>T. boeoticum</i>	PI.554656	γ	Armenia	1080	36 03'
1413*	<i>T. boeoticum</i>	PI.554657	γ	Armenia	1080	36 03'
1414*	<i>T. boeoticum</i>	PI.554658	γ	Armenia	1080	36 03'
1415*	<i>T. boeoticum</i>	PI.554659	γ	Armenia	1080	36 03'
1416*	<i>T. boeoticum</i>	PI.554660	γ	Armenia	1080	36 03'
1417*	<i>T. boeoticum</i>	PI.554661	γ	Armenia	1080	36 03'
1418*	<i>T. boeoticum</i>	PI.554662	γ	Armenia	1080	36 03'
1419*	<i>T. boeoticum</i>	PI.554663	γ	Armenia	1080	36 03'
1420*	<i>T. boeoticum</i>	PI.554664	γ	Armenia	1080	36 03'
1421*	<i>T. boeoticum</i>	PI.554665	γ	Armenia	1080	36 03'
1422*	<i>T. boeoticum</i>	PI.554666	γ	Armenia	1080	36 03'
1423*	<i>T. boeoticum</i>	PI.554667	γ	Armenia	1080	36 03'
1424*	<i>T. boeoticum</i>	PI.554668	γ	Armenia	1080	36 03'
1425*	<i>T. boeoticum</i>	PI.554669	γ	Armenia	1080	36 03'
1426*	<i>T. boeoticum</i>	PI.554670	γ	Armenia	1080	36 03'
1427*	<i>T. boeoticum</i>	PI.554671	γ	Armenia	1080	36 03'
1428*	<i>T. boeoticum</i>	PI.554672	γ	Armenia	1080	36 03'
1429*	<i>T. boeoticum</i>	PI.554673	γ	Armenia	1080	36 03'
1430*	<i>T. boeoticum</i>	PI.554674	γ	Ar		

CHAPTER 7

ID-N°	Race	Accession	Name	Source	Alt	Lat	Long
1442*	U	PI428243	<i>T. uraru</i>	USDA	600	37°12'	39°48'
1443	U	PI428244	<i>T. uraru</i>	USDA	600	37°12'	39°48'
1444*	U	PI428246	<i>T. uraru</i>	USDA	600	37°12'	39°48'
1445	U	PI428247	<i>T. uraru</i>	USDA	600	37°12'	39°48'
1446	U	PI428248	<i>T. uraru</i>	USDA	600	37°12'	39°48'
1447*	U	PI428249	<i>T. uraru</i>	USDA	500	36°56'	38°55'
1448	U	PI428251	<i>T. uraru</i>	USDA	500	36°56'	38°55'
1449	U	PI428253	<i>T. uraru</i>	USDA	1100	36°24'	44°12'
1450	U	PI428254	<i>T. uraru</i>	USDA	1975	38°44'	41°30'
1451	U	PI428255	<i>T. uraru</i>	USDA	510	37°04'	41°13'
1452	U	PI428256	<i>T. uraru</i>	USDA	701	36°55'	37°24'
1453	U	PI428261	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1454	U	PI428262	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1455*	U	PI428263	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1456	U	PI428264	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1457	U	PI428265	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1458	U	PI428266	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1459	U	PI428267	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1470*	U	PI428282	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1471	U	PI428283	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1472	U	PI428284	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1473	U	PI428285	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1474*	U	PI428286	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1475	U	PI428287	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1476	U	PI428288	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1477	U	PI428289	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1478*	U	PI428290	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1479	U	PI428291	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1480	U	PI428292	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1481	U	PI428293	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1482	U	PI428294	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1483	U	PI428295	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1484	U	PI428296	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1485	U	PI428297	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1486	U	PI428298	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1487	U	PI428299	<i>T. uraru</i>	USDA	1000	34°08'	36°08'
1488	U	PI428300	<i>T. uraru</i>	USDA	1131	34°04'	46°29'
1489	U	PI428310	<i>T. uraru</i>	USDA	1030	33°56'	36°06'
1490	U	PI428312	<i>T. uraru</i>	USDA	1050	34°02'	36°10'
1491	U	PI428313	<i>T. uraru</i>	USDA	1050	34°02'	36°10'
1492	U	PI428314	<i>T. uraru</i>	USDA	1050	34°02'	36°10'
1493	U	PI428315	<i>T. uraru</i>	USDA	1050	34°02'	36°10'
1494*	U	PI428317	<i>T. uraru</i>	USDA	1050	34°02'	36°10'
1495	U	PI428319	<i>T. uraru</i>	USDA	1050	34°02'	36°10'
1496	U	PI428337	<i>T. uraru</i>	USDA	1050	34°02'	36°10'
1497	U	PI428338	<i>T. uraru</i>	USDA	1050	34°02'	36°10'
1498	U	PI428340	<i>T. uraru</i>	USDA	1050	34°02'	36°10'
1499	U	PI428341	<i>T. uraru</i>	USDA	1050	34°02'	36°10'
1500	U	PI503318	<i>T. uraru</i>	USDA	600	37°13'	40°07'
1501	U	PI428342	<i>T. uraru</i>	USDA	600	37°13'	40°07'
1502	U	PI538724	<i>T. boeoticum</i>	USDA	600	37°13'	40°06'
1503*	U	PI538725	<i>T. uraru</i>	USDA	625	37°13'	40°01'
1504	U	PI538726	<i>T. uraru</i>	USDA	625	37°13'	40°01'
1505*	U	PI538727	<i>T. uraru</i>	USDA	600	37°11'	41°57'
1506*	U	PI538728	<i>T. uraru</i>	USDA	600	37°12'	39°48'
1507	U	PI503319	<i>T. uraru</i>	USDA	1200	37°43'49"	35°00'42"
1508*	U	PI538729	<i>T. boeoticum</i>	USDA	1200	37°43'49"	35°00'42"
1509*	U	PI538730	<i>T. uraru</i>	USDA	1200	37°43'49"	35°00'42"
1510	U	PI538731	<i>T. uraru</i>	USDA	1200	37°43'49"	35°00'42"
1511	U	PI538732	<i>T. uraru</i>	USDA	1200	37°43'49"	35°00'42"
1512	U	PI538733	<i>T. uraru</i>	USDA	1310	38°01'31"	35°31'53"
1513*	U	PI538734	<i>T. boeoticum</i>	Ozkan	760	37°48'38"	40°14'51"
1514*	U	PI538735	<i>T. boeoticum</i>	Ozkan	760	37°48'38"	40°14'51"
1515*	U	PI538736	<i>T. boeoticum</i>	Ozkan	760	37°48'38"	40°14'51"
1516*	U	PI538737	<i>T. boeoticum</i>	Ozkan	760	37°48'38"	40°14'51"
1517*	U	PI538738	<i>T. boeoticum</i>	Ozkan	760	37°48'38"	40°14'51"
1518*	U	PI538739	<i>T. boeoticum</i>	Ozkan	780	37°47'38"	40°12'14"
1519*	U	PI538740	<i>T. boeoticum</i>	Ozkan	780	37°47'38"	40°12'14"
1520*	U	PI538741	<i>T. boeoticum</i>	Ozkan	780	37°47'38"	40°12'14"

4.3	α	Turkey, 24.5 km SW from Diyarbakır to Ovadag	780	40°12'14"
4.4	α	Turkey, 24.5 km SW from Diyarbakır to Ovadag	780	40°12'14"
5-1	β	Ozkan Ozkan	900	37°47'38"
6-1	β	Turkey, 34.1 km SW from Diyarbakır to Ovadag	920	37°45'24"
6-2	β	Turkey, 18.5 km NW from Ovadag to Pirinçlik	920	37°49'17"
7-1	β	Turkey, 18.5 km NW from Ovadag to Pirinçlik	920	39°59'34"
7-2	β	Turkey, 20 km SW from Pirinçlik	1260	37°50'40"
7-3	β	Turkey, 20 km SW from Pirinçlik	1260	39°47'58"
7-4	β	Turkey, 20 km SW from Pirinçlik	1260	39°47'58"
7-5	β	Turkey, 20 km SW from Pirinçlik	1260	39°47'58"
7-6	β	Turkey, 20 km SW from Pirinçlik	1260	39°47'58"
8-1*	U	Turkey, 20 km SW from Pirinçlik	1260	39°47'58"
8-2	U	Turkey, 20 km SW from Pirinçlik	1260	39°47'58"
8-3	U	Turkey, 20 km SW from Pirinçlik	1260	39°47'58"
8-4	U	Turkey, 20 km SW from Pirinçlik	1260	39°47'58"
8-5	U	Turkey, 20 km SW from Pirinçlik	1260	39°47'58"
8-6	U	Turkey, 20 km SW from Pirinçlik	1260	39°47'58"
9-1*	β	Turkey, 2.9 km NE from Karabahçe to Pirinçlik	1300	37°49'12"
9-2*	β	Turkey, 2.9 km NE from Karabahçe to Pirinçlik	1300	39°46'29"
9-3*	α	Turkey, 2.9 km NE from Karabahçe to Pirinçlik	1300	39°46'29"
9-4*	α	Turkey, 2.9 km NE from Karabahçe to Pirinçlik	1300	39°46'29"
9-5*	α	Turkey, 29 km NE from Karabahçe to Pirinçlik	1410	37°46'42"
10-1	β	Turkey, 37.8 km SW from Pirinçlik	1410	39°46'48"
10-2	β	Turkey, 37.8 km SW from Pirinçlik	1410	39°46'48"
10-3	β	Turkey, 37.8 km SW from Pirinçlik	1410	39°46'48"
10-4	β	Turkey, 37.8 km SW from Pirinçlik	1410	39°46'48"
10-5	β	Turkey, 37.8 km SW from Pirinçlik	1410	39°46'48"
10-6	β	Turkey, 37.8 km SW from Pirinçlik	1410	39°46'48"
11-1*	α	Turkey, 41.2 km SW from Pirinçlik	1250	37°46'42"
11-2*	α	Turkey, 41.2 km SW from Pirinçlik	1250	39°44'50"
11-3*	β	Turkey, 41.2 km SW from Pirinçlik	1250	37°46'42"
11-4*	β	Turkey, 41.2 km SW from Pirinçlik	1250	39°44'50"
11-5*	β	Turkey, 41.2 km SW from Pirinçlik	1250	37°46'42"
12-1	β	Turkey, 6.3 km N from Karabahçe	1070	39°43'23"
12-2	β	Turkey, 6.3 km N from Karabahçe	1070	39°43'23"
12-3	β	Turkey, 6.3 km N from Karabahçe	1070	39°43'23"
13-1	α	Turkey, 4.6 km SW from Karabahçe	1180	37°46'19"
13-2*	β	Turkey, 4.6 km SW from Karabahçe	1180	39°44'03"
13-3*	α	Turkey, 4.6 km SW from Karabahçe	1180	39°44'03"
13-4*	α	Turkey, 4.6 km SW from Karabahçe	1180	39°44'03"
13-5	α	Turkey, 4.6 km SW from Karabahçe	1180	39°44'03"
13-6*	α	Turkey, 4.6 km SW from Karabahçe	1180	39°44'03"
13-7*	α	Turkey, 4.6 km SW from Karabahçe	1180	39°44'03"
14-1*	β	Turkey, 17.9 km SW from Karabahçe	1160	37°42'50"
14-2*	α	Turkey, 17.9 km SW from Karabahçe	1160	37°44'29"
15-1	β	Turkey, 21.7 km SW from Karabahçe	1235	37°42'51"
15-2*	β	Turkey, 21.7 km SW from Karabahçe	1235	37°42'51"
15-3	β	Turkey, 21.7 km SW from Karabahçe	1235	37°42'51"
15-4	β	Turkey, 21.7 km SW from Karabahçe	1235	37°42'51"
15-5	β	Turkey, 21.7 km SW from Karabahçe	1235	37°42'51"
15-6	β	Turkey, 21.7 km SW from Karabahçe	1235	37°42'51"
15-7	β	Turkey, 21.7 km SW from Karabahçe	1235	37°42'51"
16-1	α	Turkey, 28.1 km SW from Karabahçe	1170	37°39'49"
16-2	β	Turkey, 28.1 km SW from Karabahçe	1180	37°36'27"
17-1	α	Turkey, 33.7 km SW from Karabahçe	1150	39°42'37"
17-2	α	Turkey, 33.7 km SW from Karabahçe	1170	39°44'36"
17-3	α	Turkey, 33.7 km SW from Karabahçe	1170	39°44'36"
17-4	α	Turkey, 33.7 km SW from Karabahçe	1170	39°44'36"
17-5	α	Turkey, 33.7 km SW from Karabahçe	1170	39°44'36"
18-1	β	Turkey, 37.9 km SW from Karabahçe	1170	37°35'08"
18-2*	β	Turkey, 41.6 km SW from Karabahçe	1030	39°42'06"

CHAPTER 7

ID-N°	Race	Accession	Name	Source	Origin	Alt	Lat	Long
20-2	β		<i>T. boeoticum</i>	Ozkan	Turkey, 48.7 km SW from Karabahce	1030	37°33'09"	39°42'06"
20-3*	β		<i>T. boeoticum</i>	Ozkan	Turkey, 48.7 km SW from Karabahce	1030	37°33'09"	39°42'06"
20-4*	β		<i>T. boeoticum</i>	Ozkan	Turkey, 48.7 km SW from Karabahce	1030	37°33'09"	39°42'06"
21-1	β		<i>T. boeoticum</i>	Ozkan	Turkey, 27.6 km SW from Karacadeğ (69.6 km SW Karabahce)	950	37°33'09"	39°42'06"
22-1*	α		<i>T. boeoticum</i>	Ozkan	Turkey, 27.6 km SW from Karacadeğ (69.6 km SW Karabahce)	950	37°33'40"	39°33'40"
22-2*	β		<i>T. boeoticum</i>	Ozkan	Turkey, 27.6 km SW from Karacadeğ (69.6 km SW Karabahce)	950	37°33'40"	39°33'40"
22-3*	α		<i>T. boeoticum</i>	Ozkan	Turkey, 27.6 km SW from Karacadeğ (69.6 km SW Karabahce)	950	37°33'40"	39°33'40"
22-4*	β		<i>T. boeoticum</i>	Ozkan	Turkey, 27.6 km SW from Karacadeğ (69.6 km SW Karabahce)	950	37°33'40"	39°33'40"
22-5*	α		<i>T. boeoticum</i>	Ozkan	Turkey, 27.6 km SW from Karacadeğ (69.6 km SW Karabahce)	950	37°33'40"	39°33'40"
22-6*	α		<i>T. boeoticum</i>	Ozkan	Turkey, 27.6 km SW from Karacadeğ (69.6 km SW Karabahce)	950	37°33'40"	39°33'40"
23-1*	β		<i>T. boeoticum</i>	Ozkan	Turkey, 27.6 km SW from Karacadeğ (69.6 km SW Karabahce)	950	37°33'40"	39°33'40"
23-2*	β		<i>T. boeoticum</i>	Ozkan	Turkey, 27.6 km SW from Karacadeğ (69.6 km SW Karabahce)	950	37°33'40"	39°33'40"
23-3*	α		<i>T. boeoticum</i>	Ozkan	Turkey, 27.6 km SW from Karacadeğ (69.6 km SW Karabahce)	950	37°33'40"	39°33'40"
23-4*	β		<i>T. boeoticum</i>	Ozkan	Turkey, 27.6 km SW from Karacadeğ (69.6 km SW Karabahce)	950	37°33'40"	39°33'40"
24-1	α		<i>T. boeoticum</i>	Ozkan	Turkey, 27.1 km SE from Diyarbakır to Bismil	650	37°47'58"	40°25'35"
24-2	α		<i>T. boeoticum</i>	Ozkan	Turkey, 27.1 km SE from Diyarbakır to Bismil	650	37°47'58"	40°25'35"
24-3	α		<i>T. boeoticum</i>	Ozkan	Turkey, 27.1 km SE from Diyarbakır to Bismil	650	37°47'58"	40°25'35"
24-4	α		<i>T. boeoticum</i>	Ozkan	Turkey, 27.1 km SE from Diyarbakır to Bismil	650	37°47'58"	40°25'35"
25-1	α		<i>T. boeoticum</i>	Ozkan	Turkey, 42.2 km SE from Diyarbakır to Bismil	600	37°50'02"	40°33'51"
25-2	α		<i>T. boeoticum</i>	Ozkan	Turkey, 42.2 km SE from Diyarbakır to Bismil	600	37°50'02"	40°33'51"
25-3	α		<i>T. boeoticum</i>	Ozkan	Turkey, 42.2 km SE from Diyarbakır to Bismil	600	37°50'02"	40°33'51"
25-4	α		<i>T. boeoticum</i>	Ozkan	Turkey, 42.2 km SE from Diyarbakır to Bismil	600	37°50'02"	40°33'51"
25-5	α		<i>T. boeoticum</i>	Ozkan	Turkey, 42.2 km SE from Diyarbakır to Bismil	600	37°50'02"	40°33'51"
25-6	α		<i>T. boeoticum</i>	Ozkan	Turkey, 42.2 km SE from Diyarbakır to Bismil	600	37°50'02"	40°33'51"
26-1	α		<i>T. boeoticum</i>	Ozkan	Turkey, 9 km E from Bismil to Batman	580	37°51'03"	40°45'15"
26-2	α		<i>T. boeoticum</i>	Ozkan	Turkey, 9 km E from Bismil to Batman	580	37°51'03"	40°45'15"
26-3	α		<i>T. boeoticum</i>	Ozkan	Turkey, 9 km E from Bismil to Batman	580	37°51'03"	40°45'15"
26-4	α		<i>T. boeoticum</i>	Ozkan	Turkey, 9 km E from Bismil to Batman	580	37°51'03"	40°45'15"
26-5	α		<i>T. boeoticum</i>	Ozkan	Turkey, 9 km E from Bismil to Batman	580	37°51'03"	40°45'15"
27-1	α		<i>T. boeoticum</i>	Ozkan	Turkey, 12.8 km E from Ergani (5.3 km from Çayönü)	810	38°12'07"	39°44'37"
28-1	α		<i>T. boeoticum</i>	Ozkan	Turkey, 35.9 km NW from Siverek to Bucak	620	37°53'39"	40°00'26"
30-1	α		<i>T. boeoticum</i>	Ozkan	Turkey, 44.5 km W from Adiyaman to Besni	710	37°42'21"	37°54'55"
30-2	α		<i>T. boeoticum</i>	Ozkan	Turkey, 44.5 km W from Adiyaman to Besni	710	37°42'21"	37°54'55"
30-3	α		<i>T. boeoticum</i>	Ozkan	Turkey, 44.5 km W from Adiyaman to Besni	710	37°42'21"	37°54'55"
30-4	α		<i>T. boeoticum</i>	Ozkan	Turkey, 44.5 km W from Adiyaman to Besni	710	37°42'21"	37°54'55"
30-5	α		<i>T. boeoticum</i>	Ozkan	Turkey, 44.5 km W from Adiyaman to Besni	710	37°42'21"	37°54'55"
31-1	α		<i>T. boeoticum</i>	Ozkan	Turkey, 44.5 km W from Adiyaman to Besni	710	37°42'21"	37°54'55"
31-2	α		<i>T. boeoticum</i>	Ozkan	Turkey, 17.5 km SW from Arakan to Gaziantep	900	37°21'57"	37°32'30"
32-1*	β		<i>T. boeoticum</i>	Ozkan	Turkey, 17.5 km SW from Arakan to Gaziantep	900	37°21'57"	37°32'30"
32-2*	β		<i>T. boeoticum</i>	Ozkan	Turkey, 17.5 km SW from Arakan to Gaziantep	900	37°21'57"	37°32'30"
32-3	β		<i>T. boeoticum</i>	Ozkan	Turkey, 17.5 km SW from Arakan to Gaziantep	900	37°21'57"	37°32'30"
32-4*	β		<i>T. boeoticum</i>	Ozkan	Turkey, 17.5 km SW from Arakan to Gaziantep	900	37°21'57"	37°32'30"
32-5	β		<i>T. boeoticum</i>	Ozkan	Turkey, 17.5 km SW from Arakan to Gaziantep	900	37°21'57"	37°32'30"
32-6	β		<i>T. boeoticum</i>	Ozkan	Turkey, 17.5 km SW from Arakan to Gaziantep	900	37°21'57"	37°32'30"
32-7*	β		<i>T. boeoticum</i>	Ozkan	Turkey, 17.5 km SW from Arakan to Gaziantep	900	37°21'57"	37°32'30"
33-1*	α		<i>T. boeoticum</i>	Ozkan	Turkey, 17.5 km SW from Gaziantep to Nurdag	1010	37°10'14"	37°12'12"
33-2*	α		<i>T. boeoticum</i>	Ozkan	Turkey, 17.5 km SW from Gaziantep to Nurdag	1010	37°10'14"	37°12'12"
33-3*	α		<i>T. boeoticum</i>	Ozkan	Turkey, 17.5 km SW from Gaziantep to Nurdag	1010	37°10'14"	37°12'12"
33-4	α		<i>T. boeoticum</i>	Ozkan	Turkey, 40 km NW from Karaman to Konya	960	37°20'42"	32°48'53"
33-5	α		<i>T. boeoticum</i>	Ozkan	Turkey, 40 km NW from Karaman to Konya	960	37°20'42"	32°48'53"
33-6	α		<i>T. boeoticum</i>	Ozkan	Turkey, 40 km NW from Karaman to Konya	960	37°20'42"	32°48'53"
33-7	α		<i>T. boeoticum</i>	Ozkan	Turkey, 40 km NW from Karaman to Konya	960	37°20'42"	32°48'53"
34-1	γ		<i>T. boeoticum</i>	Ozkan	Turkey, 83 km NW Karaman to Konya (4 km from Catal Hoyuk)	1030	37°41'24"	32°48'52"
34-2	γ		<i>T. boeoticum</i>	Ozkan	Turkey, 83 km NW Karaman to Konya (4 km from Catal Hoyuk)	1030	37°41'24"	32°48'52"
34-3	γ		<i>T. boeoticum</i>	Ozkan	Turkey, 83 km NW Karaman to Konya (4 km from Catal Hoyuk)	1030	37°41'24"	32°48'52"

<i>T. boeoticum</i>	36-4	γ	37°41'24"	Turkey, 83 km NW Karaman to Konya (4 km from Catal Hoyuk)	1030
<i>T. boeoticum</i>	36-5	γ	37°41'24"	Turkey, 83 km NW Karaman to Konya (4 km from Catal Hoyuk)	1030
<i>T. boeoticum</i>	37-1	γ	37°52'49"	Turkey, 13 km from Konya to Beysehir	1240
<i>T. boeoticum</i>	38-1	γ	37°46'27"	Turkey, 11 km NW from Beysehir to Yalvac	1150
<i>T. boeoticum</i>	39-1	γ	37°53'53"	Turkey, 29 km NW from Beysehir to Yalvac	1180
<i>T. boeoticum</i>	39-2	γ	37°53'53"	Turkey, 29 km NW from Beysehir to Yalvac	1180
<i>T. boeoticum</i>	41-1	γ	38°09'57"	Turkey, Dedeceam, 67 km NW from Beysehir	1230
<i>T. boeoticum</i>	42-2*	α	37°45'33"	Turkey, 31 km SW from Basmakci to Yesilova	910
<i>T. boeoticum</i>	42-2*	α	37°45'33"	Turkey, 31 km SW from Basmakci to Yesilova	910
<i>T. boeoticum</i>	42-3	α	37°48'20"	Turkey, 31 km SW from Basmakci to Yesilova	910
<i>T. boeoticum</i>	42-4	α	37°48'20"	Turkey, 31 km SW from Basmakci to Yesilova	910
<i>T. boeoticum</i>	42-5	α	37°48'20"	Turkey, 31 km SW from Basmakci to Yesilova	910
<i>T. boeoticum</i>	43-1	γ	37°48'20"	Turkey, 31 km SW from Basmakci to Yesilova	1240
<i>T. boeoticum</i>	45-2	γ	37°11'35"	Turkey, 5 km E from Bozkir to Karanam	1070
<i>T. boeoticum</i>	46-1*	α	37°19'31"	Turkey, 42 km E from Turkoglu to Gaziantep	710
<i>T. boeoticum</i>	46-2*	β	37°19'31"	Turkey, 42 km E from Turkoglu to Gaziantep	710
<i>T. boeoticum</i>	46-3*	β	37°19'31"	Turkey, 42 km E from Turkoglu to Gaziantep	710
<i>T. boeoticum</i>	48-1	α	37°15'59"	Turkey, 57 km SE from Turkoglu to Gaziantep	860
<i>T. boeoticum</i>	49-1*	α	37°17'33"	Turkey, 60 km SE from Turkoglu	845
<i>T. boeoticum</i>	49-2*	α	37°17'33"	Turkey, 60 km SE from Turkoglu	845
<i>T. boeoticum</i>	50-1*	β	37°17'51"	Turkey, 61 km SE from Turkoglu	840
<i>T. boeoticum</i>	50-2*	β	37°17'51"	Turkey, 61 km SE from Turkoglu	840
<i>T. boeoticum</i>	50-3*	β	37°17'51"	Turkey, 61 km SE from Turkoglu	840
<i>T. boeoticum</i>	51-1	β	37°18'53"	Turkey, 63 km SE from Turkoglu	840
<i>T. boeoticum</i>	51-2	β	37°18'53"	Turkey, 63 km SE from Turkoglu	840
<i>T. boeoticum</i>	52-1	β	37°19'46"	Turkey, 72 km SE from Turkoglu	800
<i>T. boeoticum</i>	52-2	β	37°19'46"	Turkey, 72 km SE from Turkoglu	800
<i>T. boeoticum</i>	53-1	β	37°19'46"	Turkey, 72 km SE from Turkoglu	800
<i>T. boeoticum</i>	53-2	β	37°19'46"	Turkey, 72 km SE from Turkoglu	800
<i>T. boeoticum</i>	53-3	β	37°19'46"	Turkey, 72 km SE from Turkoglu	800
<i>T. boeoticum</i>	56-1*	β	37°17'39"	Turkey, 39 km ESE from Narliu (SW of Karadag)	760

Abbreviations as in Supplementary table S2

Supplementary Table S2. Details and collection sites for 452 lines that were sequenced for 18 loci

ID-N°	Race	ident	Accession	Name	Source	Origin	Alt	Lat	Long
4	M		P194740	<i>T. monococcum</i>	Can/A	Spain, Valki Exp. Station	40 00'	04 00'	04 00'
5	M		PI119435	<i>T. monococcum</i>	Can/A	Turkey, 20 km W Samsun, field	289	41 12'	36 11'
7	M		PI167615	<i>T. monococcum</i>	Can/A	Turkey, Balikesir, Okuegerli	20	40 03'	28 10'
8*	M	492	PI167625	<i>T. monococcum</i>	Can/A	Turkey, Balikesir, seed store in Bandirma	29	40 20'	27 58'
14*	M	15	P1254195	<i>T. monococcum</i>	Can/A	Turkey, Ankara, Yenisehir	1002	39 55'	32 52'
15	M		P1264935	<i>T. monococcum</i>	Can/A	Greece, Crete, Mesava Plain Exp. Station	146	35 02'	25 00'
26	M		PI306532	<i>T. boeoticum</i>	Can/A	Romania, Botanical Garden?	46 00'	25 00'	
49*	α	489	PGR 10805	<i>T. boeoticum</i>	Can/A	Iraq, Arbil, 1 km NE of Salahadin	1100	36 24'	44 12'
69*	M	120	G 4325	<i>T. monococcum</i> <i>sinskajae</i>	Can/A	originally from Turkey			
102	M		TRI 612/74 SKL	<i>T. monococcum</i> var. <i>softianum</i>	IPK	Albania, Kelyra, Vjossa valley			
104	M		TRI 618/74 SKL	<i>T. monococcum</i> var. <i>vulgare</i>	IPK	Albania, Kelyra, Vjossa valley			
109*	M	538	TRI 1990/74 SKL	<i>T. monococcum</i> var. <i>vulgare</i>	IPK	Albania, Prevs			
115	M		TRI 3637/74 SKL	<i>T. monococcum</i> <i>vulgare</i>	IPK	Hungary?			
120	M		TRI 1125/76 SKL	<i>T. monoc. sinkajae filat</i>	IPK	originally from Turkey			
123#	ae		A Schgl1/88	<i>T. boeoticum</i> <i>rufinigrum</i>	IPK	Armenia			
127#	M		AT 129/10/89	<i>T. monococcum</i> <i>sinskajae</i>	IPK	originally from Turkey			
137+	M		BGRC 2521	<i>T. monococcum</i> <i>ereditatum</i>	BGRC	Albania, Kelyra, Vjossa valley			
152+	M		BGRC 7038	<i>T. monococcum</i> <i>horenmannii</i>	BGRC	GDPR			
187	M		BGRC 13182	<i>T. monococcum</i> <i>vulgare</i>	BGRC	Italy			
189*	M	102	BGRC 13187	<i>T. monococcum</i> <i>sofianum</i>	BGRC	Balkans			
190	M		BGRC 13189	<i>T. monococcum</i> <i>nigricutum</i>	BGRC	Balkans			
194	M		BGRC 13193	<i>T. monococcum</i> <i>horenmannii</i>	BGRC	Austria, Vorarlberg			
197	M		BGRC 13196	<i>T. monococcum</i> <i>ereditatum</i>	BGRC	Austria, Vorarlberg			
209*	M	538	BGRC 20451	<i>T. monococcum</i> <i>nigricutum</i>	BGRC	Balkans			
210+	ae		BGRC 20518	<i>T. boeoticum</i> <i>larijanovi</i>	BGRC	Balkans			
211	M		BGRC 20521	<i>T. monococcum</i> <i>pseudoaffrascens</i>	BGRC	Balkans			
226+	ae		BGRC 36546	<i>T. boeoticum</i> <i>zuccarini</i> <i>aiglopoides</i>	MP-L-Cologne	Balkans			
227+	ae		BGRC 36547	<i>T. boeoticum</i> <i>zuccarini</i> <i>aiglopoides</i>	MP-L-Cologne	Balkans			
228	ae		BGRC 36548	<i>T. boeoticum</i> <i>maysuntiani</i> <i>aiglopoides</i>	MP-L-Cologne	Balkans			
229	γ		BGRC 36551	<i>T. boeoticum</i> <i>maysuntiani</i> <i>aiglopoides</i>	MP-L-Cologne	Balkans			
233#	M		BGRC 36556	<i>T. monococcum</i> <i>leptissimum</i>	MP-L-Cologne	Bulgaria			
259	M		BGRC 37351	<i>T. monococcum</i> <i>albohornemannii</i>	MP-L-Cologne	Germany			
269	M		BGRC 42006	<i>T. monococcum</i> <i>vulgare</i>	MP-L-Cologne	Sweden			
279*	M	190	BGRC 42016	<i>T. monococcum</i> <i>nigricutum</i>	MP-L-Cologne	Balkans			
280+	M		BGRC 42019	<i>T. monococcum</i> <i>macedonicum</i>	MP-L-Cologne	Albania, Kelyra, Vjossa valley			
282	M		BGRC 42019	<i>T. monococcum</i> <i>horenmannii</i>	MP-L-Cologne	Spain			
303*	M	355	BGRC 43448	<i>T. monococcum</i> <i>flavescens</i>	MP-L-Cologne	France			
306	M		BGRC 43451	<i>T. monococcum</i> <i>macedonicum</i>	MP-L-Cologne	Balkans			
309	M		BGRC 43454	<i>T. monococcum</i> <i>horenmannii</i>	MP-L-Cologne	Germany			
311	M		BGRC 43456	<i>T. monococcum</i> <i>maysuntiani</i> <i>horenmannii</i>	MP-L-Cologne	Germany			
314	M		BGRC 43459	<i>T. monococcum</i> <i>horenmannii</i>	MP-L-Cologne	Switzerland			
320+	M		BGRC 43466	<i>T. monococcum</i> <i>macedonicum</i>	MP-L-Cologne	Albania			
328	M		BGRC 43474	<i>T. monococcum</i> <i>flavescens</i>	MP-L-Cologne	Balkans			
351*	M	521	BGRC 43497	<i>T. monococcum</i> <i>albohornemannii</i>	MP-L-Cologne	Germany			
353	M		BGRC 43499	<i>T. monococcum</i> <i>horenmannii</i>	MP-L-Cologne	Syria			
355	M		BGRC 43501	<i>T. monococcum</i> <i>horenmannii</i>	MP-L-Cologne	Romania			
379*	α	1116	198	<i>T. monococcum</i> <i>bocoticum</i>	USA/KS	Lebanon, El Beqa, between Kfar kouk and A'ha	1508	33 31'	35 52'
386	α		747	<i>T. boeoticum</i>	USA/KS	Turkey, Urfa, 83.8 km W of Kiziltepe	670	37 14'	39 41'
388	U		787	<i>T. urartu</i>	USA/KS	Lebanon, El Beqa, Talia	1030	33 56'	36 06'
393	U		831	<i>T. urartu</i>	USA/KS	Iran, Bakhtaran, 6 km S Shahabad	1131	34 04'	46 29'
394	U		851	<i>T. urartu</i>	USA/KS	Armenia	40 30'	45 00'	
396*	M	584	2701	<i>T. monococcum</i>	USA/KS				
431	α		1983	<i>T. boeoticum</i>	Austral.				
432*	M	102	19842	<i>T. monococcum</i> <i>softianum</i>	Austral.				
433	M		19846	<i>T. monococcum</i> <i>flavescens</i>	Austral.				
435	M		19852	<i>T. monococcum</i> <i>var. macedonicum</i>	Austral.				
476	M		90451	<i>T. monococcum</i> <i>var. macedonicum</i>	USA/DA				
489	α		Clt 17673	<i>T. boeoticum</i>	USA/DA				
492	M		PI 119423	<i>T. monococcum</i>	USA/DA				
493*	M	492	PI 119435	<i>T. monococcum</i>	USA/DA	Turkey, 20 km W Samsun, field	289	39 57'	36 11'

ID-N°	Race	ident	Accession	Name	Source	Origin	Alt	Lat	Long
746	α		P1427614	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 62 to 71.9 km E of Urfa	662	37°14'	39°23'
751	β		P1427619	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 16 km E of Siverek	1050	37°43'	39°28'
752	β		P1427620	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 16 km E of Siverek	1050	37°43'	39°28'
753	α		P1427621	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakir, 20.2 km E of Siverek	1200	37°43'	39°30'
754	β	758	P1427622	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakir, 52.5 km W of Diyarbakir in the Karacadag	1400	37°47'	39°46'
755*	β		P1427626	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakir, 52.5 km W of Diyarbakir in the Karacadag	1400	37°47'	39°46'
758	β		P1427627	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20.2 km E of Siverek	1200	37°43'	39°30'
760	β		P1427629	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20.2 km E of Siverek	1200	37°43'	39°30'
763	β		P1427632	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20.2 km E of Siverek	1200	37°43'	39°30'
765	β		P1427634	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20.2 km E of Siverek	1200	37°43'	39°30'
766	β		P1427635	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20.2 km E of Siverek	1200	37°43'	39°30'
767	β		P1427636	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20.2 km E of Siverek	1200	37°43'	39°30'
768	β		P1427640	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahaddin	1100	36°24'	44°12'
771*	α	1062	P1427644	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahaddin	1100	36°24'	44°12'
775*	α	489	P1427644	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahaddin	1100	36°24'	44°12'
777	α		P1427646	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahaddin	1100	36°24'	44°12'
779*	α	830	P1427648	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahaddin	1100	36°24'	44°12'
780*	α	1252	P1427651	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahaddin	1100	36°24'	44°12'
784	α		P1427653	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahaddin	1100	36°24'	44°12'
787*	α	944	P1427656	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahaddin	1100	36°24'	44°12'
790*	α	489	P1427659	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahaddin	1100	36°24'	44°12'
795	α		P1427664	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahaddin	1100	36°24'	44°12'
797*	α	1182	P1427666	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahaddin	1000	36°25'	44°22'
800	α		P1427669	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 4 km NE of Shadlawa	1000	36°25'	44°22'
803*	α	827	P1427672	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 4 km NE of Shadlawa	1000	36°25'	44°22'
807*	α	986	P1427676	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 21 km S of Harran	1000	36°25'	44°22'
815*	α	986	P1427684	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 21 km S of Harran	1000	36°25'	44°22'
818*	α	827	P1427688	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 21 km W of Shadlawa	1000	36°20'	44°11'
821*	α	827	P1427691	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadlawa	1000	36°23'	44°14'
824*	α	834	P1427694	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadlawa	1000	36°23'	44°14'
827	α		P1427697	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadlawa	1000	36°23'	44°14'
830	α		P1427700	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadlawa	1000	36°23'	44°14'
834	α		P1427704	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadlawa	1000	36°23'	44°14'
839*	α	827	P1427709	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadlawa	1000	36°23'	44°14'
840	α		P1427710	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadlawa	1000	36°23'	44°14'
843*	α	1011	P1427713	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadlawa	1000	36°23'	44°14'
862	α		P1427733	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadlawa	950	36°58'	43°11'
864*	α	1037	P1427735	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadlawa	1250	36°58'	43°11'
868	α		P1427739	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadlawa	1250	36°58'	43°11'
870*	α	871	P1427741	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 6 km E of Suara Tuka	1050	37°00'	43°13'
871	α		P1427742	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 6 km E of Suara Tuka	750	36°55'	43°02'
875	α		P1427747	<i>T. boeoticum</i>	USDA	Iraq, Duhuk, 5.5 km N of Duhuk	1380	36°55'	43°02'
895*	α	1194	P1427768	<i>T. boeoticum</i>	USDA	Iraq, Duhuk, 24.5 km NE of Duhuk	950	36°58'	43°11'
906	α		P14277735	<i>T. boeoticum</i>	USDA	Iraq, Duhuk, 2 km W of Suara Tuka	700	35°47'	45°08'
907	α		P14277739	<i>T. boeoticum</i>	USDA	Iraq, Duhuk, 2 km W of Suara Tuka	700	35°47'	45°08'
909	α		P14277780	<i>T. boeoticum</i>	USDA	Iraq, Duhuk, 6 km E of Suara Tuka	1561	34°17'	46°13'
910*	α	1057	P14277782	<i>T. boeoticum</i>	USDA	Iraq, Duhuk, 25 km E of Sulaimaniyah	960	35°41'	45°39'
923	α		P14277783	<i>T. boeoticum</i>	USDA	Iraq, Duhuk, between Zawita and Suara Tuka	1500	34°04'	46°29'
925	α		P14277786	<i>T. boeoticum</i>	USDA	Iraq, As Sulaymaniyah, 44 km NW of Sulaimaniyah	1900	34°50'	47°10'
935	α		P14277788	<i>T. boeoticum</i>	USDA	Iraq, As Sulaymaniyah, 44 km NW of Sulaimaniyah	1400	34°23'	44°12'
936	α		P14277790	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 36 km NW of Shahabad	1100	36°24'	44°12'
938	α		P14277811	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabad,	1100	36°24'	44°12'
939+	α		P14277812	<i>T. boeoticum</i>	USDA	Iraq, Bakhtaran, 6 km S of Shahabad,	1100	36°24'	44°12'
941*	α	1057	P14277814	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NW of Salahadin	1100	36°24'	44°12'
944	α		P14277817	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahadin	1100	36°24'	44°12'
947*	α	753	P14277820	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahadin	1100	36°24'	44°12'
953*	α	827	P14277826	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahadin	1100	36°24'	44°12'
956*	α	1062	P1427829	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahadin	1100	36°24'	44°12'
960*	α	1057	P1427833	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 2 km NW of Salahadin	1100	36°24'	44°14'
965*	α	834	P1427838	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 2 km NW of Salahadin	1100	36°24'	44°14'
968*	α	49-1	P1427841	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 2 km NW of Salahadin	1100	36°24'	44°14'
969*	α	489	P1427842	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 4 km NE of Shadlawa	1000	36°25'	44°22'
972*	α	795	P1427845	<i>T. boeoticum</i>	USDA				

CHAPTER 7

ID-N°	Race	ident	Accession	Name	Source	Origin	Alt	Lat	Long
1144*	α	1106	P1470726	<i>T. boeoticum</i>	USDA	Turkey, Elazig, 25 km SW of Elazig	1160	38°32'	39°02'
1148	α		P1503302	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 16 km W of Kiziltepe	800	37°14'	39°23'
1150	α		P1503304	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 52.5 km NE of Urfa, near Hilvan	650	37°33'	38°55'
1151*	α	1252	P1503305	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahadin	1100	36°24'	44°12'
1153	α		P1503307	<i>T. boeoticum</i>	USDA	Iraq, Dohuk, 24 km NE of Dohuk	950	36°58'	43°11'
1156*	α	925	P1503578	<i>T. boeoticum</i>	USDA	Iran, Bakhtaran, 47 km NW of Shahabad	1500	34°20'	46°08'
1161*	α	49-1	P1538327	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 80.5 km W of Kiziltepe	670	37°14'	39°43'
1166	α		P1538332	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 2.9 km S of Viranshehir	600	37°13'	39°47'
1170*	α	723	P1538356	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 52.5 km NE of Urfa, near Hilvan	650	37°33'	38°55'
1174	β		P1538340	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakir, 52.5 km W of Diyarbakir in the Karacadag	1400	37°47'	39°46'
1179*	α	999	P1538345	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 2 km NW of Salahaddin	1100	36°24'	44°14'
1181*	α	795	P1538347	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 6 km NE of Shadawa	1000	36°25'	44°22'
1182	α		P1538348	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 4 km NE of Shadawa	1000	36°23'	44°14'
1187*	α	999	P1538353	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadawa	1000	36°23'	43°02'
1190*	α	1020	P1538356	<i>T. boeoticum</i>	USDA	Iraq, Dohuk, 5.5 km N of Dohuk	750	36°55'	43°11'
1194	α		P1538360	<i>T. boeoticum</i>	USDA	Iraq, Dohuk, 24 km NE of Dohuk towards Amadiya	950	36°58'	43°11'
1196	α		P1538362	<i>T. boeoticum</i>	USDA	Iraq, Dohuk, 2 km W of Shadawa	1250	36°58'	43°11'
1199*	α	871	P1538365	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 6 km E of Shadawa	1050	37°00'	43°13'
1201	α		P1538367	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 6 km E of Shadawa	1050	37°00'	43°13'
1204	α		P1538370	<i>T. boeoticum</i>	USDA	Iraq, Dohuk, between Zawita and Suira Tuka	1380	36°58'	43°11'
1207	α		P1538373	<i>T. boeoticum</i>	USDA	Iraq, Dohuk, between Zawita and Suira Tuka	1380	36°58'	43°11'
1210*	α	1211	P1538376	<i>T. boeoticum</i>	USDA	Iran, Bakhtaran, 5.5 km N of Bisotun	1350	34°26'	47°26'
1211	α		P1538377	<i>T. boeoticum</i>	USDA	Iran, Bakhtaran, 5.5 km N of Bisotun	1350	34°26'	47°26'
1213*	α	1252	P1538365	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahadin	1100	36°24'	44°12'
1215*	α	489	P1538367	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahadin	1100	36°24'	44°12'
1220*	α	986	P1538386	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 21 km S of Harran	1000	36°25'	44°22'
1221	α		P1538387	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadawa	1000	36°25'	44°22'
1222	α		P1538388	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadawa	1000	36°23'	44°14'
1225*	α	999	P1538391	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadawa	1000	36°23'	44°14'
1228*	α	827	P1538394	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadawa	1000	36°23'	44°14'
1231*	α	999	P15383981	<i>T. boeoticum</i>	USDA	Iraq, Dohuk, 6 km E of Shadawa	1000	36°23'	44°14'
1235*	α	871	P1538397	<i>T. boeoticum</i>	USDA	Iraq, Dohuk, 6 km E of Shadawa	1050	37°00'	43°13'
1238*	α		P1538404	<i>T. boeoticum</i>	USDA	Iraq, Dohuk, 6 km E of Shadawa	1050	37°00'	43°13'
1239	α		P1538405	<i>T. boeoticum</i>	USDA	Iraq, As Salaymaniyah, 43 km NW of Sulaimaniyah near Sardash	800	35°47'	45°08'
1240*	α	1059	P1538406	<i>T. boeoticum</i>	USDA	Iraq, As Salaymaniyah, 12 km S of Sulaimaniyah	832	35°29'	45°32'
1241*	α	1166	P1538407	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 2.9 km S of Viranshehir	600	37°13'	39°47'
1245	α		P1538407	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 1 km NE of Salahadin	1100	36°24'	44°14'
1247	α		P1538401	<i>T. boeoticum</i>	USDA	Iraq, Dohuk, 2 km W of Shadawa	1250	36°58'	43°11'
1250	α		P1538416	<i>T. boeoticum</i>	USDA	Iraq, Arbil, 13 km W of Shadawa	1000	36°23'	44°14'
1252	α		P1538419	<i>T. boeoticum</i>	USDA	Turkey, Yozgat, 48 km SE of Sorgun	1100	39°41'	35°40'
1256	γ		P1538423	<i>T. boeoticum</i>	USDA	Turkey, Bolu, 10 km E Mengen	700	40°59'	32°11'
1258	α		P1538425	<i>T. boeoticum</i>	USDA	Turkey, Denizli, Acipayam?	1160	37°25'	29°22'
1259	M		P1538721	<i>T. monococcum</i>	USDA	Turkey, Çanakkale, Ecebat	52	40°11'	26°21'
1260	M		P1538722	<i>T. monococcum</i>	USDA	Turkey, Tekirdag, Malkara	234	40°53'	26°54'
1261	γ		P1538723	<i>T. boeoticum</i>	USDA	Turkey, Edirne, Edirne	85	41°40'	26°34'
1265	α		P1554480	<i>T. boeoticum</i>	USDA	Turkey, Gaziantep, 1 km S of Araban village, 25 km N Yavuzeli	550	37°26'	37°41'
1271	α		P1554487	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakir, 8 km SW of Dicle	950	37°37'	39°33'
1272	α		P1554488	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 28 km E of Siverek	1050	37°43'	39°35'
1273	α		P1554491	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 3 km N of Hilvan	600	37°37'	38°57'
1274	α		P1554493	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 3 km SW of Hilvan	600	37°34'	38°56'
1279	α		P1554503	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakir, Al spring, 7 km S of Cinar (S of Diyarbakir)	625	37°39'	40°28'
1280	α		P1554504	<i>T. boeoticum</i>	USDA	Turkey, Diyarbakir, Al spring, 7 km S of Cinar (S of Diyarbakir)	625	37°39'	40°28'
1281	α		P1554505	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 20 km SE of Siverek	450	37°37'	39°33'
1282	α		P1554488	<i>T. boeoticum</i>	USDA	Turkey, Urfa, 5 km NW of Urfa-Diyarbakir road junction	500	37°16'	38°46'
1283	α		P1554521	<i>T. boeoticum</i>	USDA	Turkey, Izmit, 0.5 km E of Aliaga, E edge of village	60	38°48'	26°59'
1289	γ		P1554522	<i>T. boeoticum</i>	USDA	Turkey, Izmit, 0.5 km E of Aliaga, E edge of village	60	38°48'	26°59'
1290	γ		P1554523	<i>T. boeoticum</i>	USDA	Turkey, Canakkale, 7 km NE of Canakkale on route to Lapseki	80	40°11'	26°28'
1291	γ		P1554525	<i>T. boeoticum</i>	USDA	Turkey, Bursa, 11 km N of Yenisehir	370	40°22'	29°41'
1294	γ		P1554531	<i>T. boeoticum</i>	USDA	Turkey, Çankırı, 8 km E of Çekerek	1000	40°49'	32°59'
1296	γ	1296	P1554532	<i>T. boeoticum</i>	USDA	Turkey, Çankırı, 19 km S of Çankırı	710	40°29'	33°40'
1296	γ		P1554533	<i>T. boeoticum</i>	USDA	Turkey, Ankara, 12 km NE of Ankara City limit sign	900	40°02'	32°55'
1297	γ		P1554535	<i>T. boeoticum</i>	USDA	Turkey, Ankara, 5 km E of Ankara City limit sign	575	39°56'	32°56'

<i>T. boeoticum</i>	PI 554537	Y	99	Y	USDA	Turkey, 40 km SW Ankara, 3.5 km N Haymana, Haymana road
	PI 554538	00+	00+	Y	USDA	Turkey, Ankara, 8.5 km N of Haymana station
	PI 554539	01	01	Y	USDA	Turkey, Ankara, 8.5 km N of Haymana station
	PI 554540	02*	02*	Y	USDA	Turkey, 31 km S Ankara, 12.5 km N Haymana, Haymana road
	PI 554542	03*	03+	Y	USDA	Turkey, Ankara, 25 km S of Golbasi
	PI 554543	04	04	Y	USDA	Turkey, Konya, 32 km W of Konya
	PI 554545	05	05	Y	USDA	Turkey, Konya, 27 km NE of Haymana station
	PI 554546	06	06	Y	USDA	Turkey, Konya, 6 km SW of Beysehir
	PI 554547	07	07	Y	USDA	Turkey, Konya, 5 km N of Beysehir
	PI 554548	08#	08#	Y	USDA	Turkey, Konya, 5 km N of Beysehir
	PI 554549	09#	09#	Y	USDA	Turkey, Konya, 5 km N of Beysehir
	PI 554550	10	10	Y	USDA	Turkey, Konya, 5 km N of Beysehir
	PI 554551	11	11	Y	USDA	Turkey, Konya, 18 km N of Beysehir
	PI 554552	12	12	Y	USDA	Turkey, Isparta, 1.5 km NW of Egirdir
	PI 554553	13	13	α	USDA	Turkey, Burdur, 11 km NE of Yesilova
	PI 554554	14	14	α	USDA	Turkey, Burdur, 11 km NE of Yesilova
	PI 554558	15	15	α	USDA	Turkey, Burdur, 11 km NE of Yesilova
	PI 554559	16#	16#	Y	USDA	Turkey, Denizli, 32 km S of Denizli, junction to Tavas
	PI 554560	17	17	Y	USDA	Turkey, Kirsehir, 12 km NW of Kirsehir province border
	PI 554561	18	18	Y	USDA	Turkey, Kirsehir, 12 km NW of Kirsehir
	PI 554562	19	19	Y	USDA	Turkey, Kayseri, 12 km W of Bayanyurt
	PI 554565	20#	20#	Y	USDA	Turkey, Kayseri, 6 km N of Pinharbası
	PI 554566	21+	21+	α	USDA	Turkey, Elazig, 1 km E of Arapkir-Elazig junction toward Elazig
	PI 554571	22	23	α	USDA	Turkey, Elazig, 5 km E of Tunceli-Bingol junction
	PI 554573	24	24	α	USDA	Turkey, Elazig, 11 km W of Elazig-Bingol province border
	PI 554574	25	25	Y	USDA	Turkey, Van, 6 km SE of Van
	PI 554575	26	26	α	USDA	Turkey, Hakkarı, 21 km SW of Semendili
	PI 554577	31	31	M	MG 4278	Italy, Latium
	MG 4278	1395	U	U	101001	Armenia
	1310	309	78	M	UK	MPI-Cologne
	79*	79*	M	MPi-Cologne	VIR	originally from Turkey
	92#	92#	M	VIR	Armenia	Turkey, Mardin, 44.5 km W of Kiziltepe
	95	95	U	USDA	Turkey, Mardin, 44.5 km W of Kiziltepe	
	96*	U	1408	USDA	Turkey, Mardin, 44.5 km W of Kiziltepe	
	99*	U	1408	USDA	Turkey, Mardin, 44.5 km W of Kiziltepe	
	100*	U	1408	USDA	Turkey, Mardin, 44.5 km W of Kiziltepe	
	101*	U	1408	USDA	Turkey, Mardin, 44.5 km W of Kiziltepe	
	104	U	1408	USDA	Turkey, Mardin, 44.5 km W of Kiziltepe	
	108	U	1408	USDA	Turkey, Mardin, 44.5 km W of Kiziltepe	
	113	U	1404	USDA	Turkey, Mardin, 53.8 km W of Kiziltepe	
	116*	U	1404	USDA	Turkey, Mardin, 53.8 km W of Kiziltepe	
	23	α	1550	USDA	Turkey, Mardin, 53.8 km W of Kiziltepe	
	25*	U	1550	USDA	Turkey, Mardin, 49.3 km E of Kiziltepe	
	27	U	PI 428226	USDA	Turkey, Urfa, 5.4 km S of Viransehir	
	42	U	PI 428243	USDA	Turkey, Urfa, 5.4 km S of Viransehir	
	44*	U	1408	USDA	Turkey, Urfa, 28.8 km S of Urfa	
	47	U	PI 428246	USDA	Turkey, Urfa, 28.8 km S of Urfa	
	55*	U	1462	USDA	Turkey, Mardin, 45.9 km W of Kiziltepe	
	55*	U	PI 428263	USDA	Turkey, Mardin, 45.9 km W of Kiziltepe	
	61	U	PI 428269	USDA	Turkey, Urfa, 5.4 km S of Viransehir	
	62	U	PI 428270	USDA	Turkey, Urfa, 5.4 km S of Viransehir	
	63*	U	1550	USDA	Turkey, Urfa, 5.4 km S of Viransehir	
	65*	U	PI 428271	USDA	Turkey, Urfa, 6 km S of Shahabad,	
	66*	U	1462	USDA	Turkey, Urfa, 6 km S of Shahabad,	
	78*	U	PI 428282	USDA	Turkey, Urfa, 6 km S of Shahabad,	
	78*	U	PI 428286	USDA	Turkey, Urfa, 6 km S of Shahabad	
	1462	U	PI 428293	USDA	Turkey, Urfa, 6 km S of Shahabad	
	1550	U	PI 428315	USDA	Turkey, Urfa, 6 km S of Shahabad	
	1550	U	PI 428317	USDA	Turkey, Urfa, 6 km S of Shahabad	
	388	U	PI 428327	USDA	Turkey, Urfa, 6 km S of Shahabad	
	46	U	PI 428341	USDA	Turkey, Urfa, 6 km S of Shahabad	
	46	U	PI 503318	USDA	Turkey, Urfa, 6 km S of Shahabad	
	29	α	1442	USDA	Turkey, Urfa, 6 km S of Shahabad	
	30*	U	PI 538724	USDA	Turkey, Mardin, 44.5 km W of Kiziltepe	
	33*	U	PI 538728	USDA	Turkey, Urfa, 5.4 km S of Viransehir	
	35	U	PI 538730	USDA	Turkey, Urfa, 5.4 km S of Viransehir	
	38	U	PI 538733	USDA	Turkey, Urfa, 5.4 km S of Viransehir	
	46	U	PI 538741	USDA	Turkey, Urfa, 6 km S of Shahabad	
	47	U	PI 538742	USDA	Turkey, Urfa, 6 km S of Shahabad	
	48*	U	PI 538743	USDA	Turkey, Urfa, 6 km S of Shahabad	
	50*	U	PI 538745	USDA	Turkey, Urfa, 6 km S of Shahabad	
	1550	U	PI 538746	USDA	Turkey, Urfa, 6 km S of Shahabad	

49-1	α	49-1	<i>T. boeoticum</i>	Özkan	Turkey, 60 km SE from Türkoglu	845	37°17'33"
49-2*	α	49-1	<i>T. boeoticum</i>	Özkan	Turkey, 60 km SE from Türkoglu	845	37°17'33"
50-3*	β	50-3	<i>T. boeoticum</i>	Özkan	Turkey, 61 km SE from Türkoglu	840	37°14'42"
50-2	β	50-3	<i>T. boeoticum</i>	Özkan	Turkey, 61 km SE from Türkoglu	840	37°14'55"
50-3	β	50-3	<i>T. boeoticum</i>	Özkan	Turkey, 61 km SE from Türkoglu	840	37°14'55"
56-1	β	56-3	<i>T. boeoticum</i>	Özkan	Turkey, 39 km ESE from Narlu (SW of Karadag)	760	37°17'06"
56-2*	β	56-3	<i>T. boeoticum</i>	Özkan	Turkey, 39 km ESE from Narlu (SW of Karadag)	760	37°17'39"
56-3	β	56-3	<i>T. boeoticum</i>	Özkan	Turkey, 39 km ESE from Narlu (SW of Karadag)	760	37°17'39"

Abbreviations and notes

One-hundred-thirty redundant lines (same haplotype combinations over 17 loci, without *Lr10*) are marked with an asterisk, *“.

For figure 2B these 130 redundant lines, as well as all remaining *T. urartu* lines and all heterozygous lines were excluded.

Heterozygous lines are marked with „+“.

Lines with missing loci informations (without *Lr10*) are marked with „#“.

ID-N° Lines with missing loci informations (without *Lr10*) are marked with „#“.

Race Identification number within the line collection at the MPIZ in Cologne

Accession *T. m. boeoticum* races α , β , γ , *T. m. monococcum* (M), *T. m. aegilopoides* (ae), *T. urartu* (U)

Name Seedbank accession numbers

Source Species name, based on seedstore informations

Seeds source:

Austral. Australian Winter Cereals Collection, Tamworth, Australia

BGRC Institut für Pflanzenbau und Pflanzenzüchtung, Braunschweig, Germany

Brandolini Andrea Brandolini, CRA-Experimental Institute for Cereal Research, S. Angelo L. (LO), Italy

Can/ A University of Alberta, Edmonton, Canada

IdG Istituto del Germoplasma, Bari, Italy

IPK Institut für Genetik und Kulturpflanzenforschung, Gatersleben, Germany

MPI-Cologne Max-Planck-Institut für Züchtungsforschung, Köln, Germany

Özkan Hakan Özkan, Çukurova University, Adana, Turkey

Pena-Chocarro L. Peña Chocarro, Consejo Superior de Investigaciones Científicas, Madrid, Spain

UK Cambridge Laboratory, Norwich, UK

USA/KS Kansas State University, Manhattan, Kansas, USA

USDA National Small Grain Collection, Aberdeen, Idaho, USA

VIR Vavilov All Union Institute of Plant Industry, S. Petersburg, Russia

Origin collection sites or origin

Alt altitude

Lat latitude

Lon longitude

Supplementary Table S3. Loci, sequence-source, chromosomal position, and function

Symbol	Gene-locus	Sequence-Source	Chr	Function
<i>BAMY1</i>	beta-amylase, b-Amy1	EST-clon 130	4AL or 5A (Ainsworth et al. 1983)	Degradation of starch
<i>GAPDH</i>	glyceraldehyde-3-phosphate-DH, cytosolic	EST-clon 473	7A (Chao et al. 1989)	Glycolysis
<i>ACCI</i>	acetyl-CoA-carboxylase, plastid	(Huang et al. 2002)	2AS (Gornicki et al. 1997)	Fatty acid biosynthesis
<i>PGK1</i>	3-phosphoglycerate kinase, plastid	(Huang et al. 2002)	1A (Chao et al. 1989)	Calvin cycle
<i>AGPL</i>	ADP-glucose-pyrophosphorylase, agp2, cytosolic	EST-clon 563	1AL (Ainsworth et al. 1995)	Seed yield, starch biosynthesis
<i>CesA</i>	cellulose synthase A	EST-clon 548	6A (Burton et al. 2004)	Cellulose synthesis, cell wall biosynthesis
<i>6SFT</i>	fructosyltransferase like or vacuolar invertase like	EST-clon 579	1A or 4A or 7A (Chalmers et al. 2005)	Fructan synthesis, drought and cold-stress tolerances
<i>BADH</i>	betaine aldehyde dehydrogenase	EST-clones 174, 462	7A (Cattivelli et al. 2002)	Osmoprotection
<i>PEPC</i>	phosphoenolpyruvate carboxylase	(Gonzalez et al. 1998)	3A or 7A (Chao et al. 1989)	Multiple physiological roles, anaplerotic function
<i>G6PDH</i>	glucose-6-phosphate-DH, cytosolic	(Nemoto et al. 1999)	2A (Nemoto et al. 2000)	PPC-pathway, OPP-pathway, salt stress responses
<i>GPT</i>	glucose-6-phosphate/ phosphate translocator	EST-clon 28-G07, AF548741	Nm	Starch biosynthesis, oxidative pentose phosphate pathway
<i>pinB</i>	puroindoline b	EST-clon 186	5AS (Tranquilli et al. 1999)	Grain texture, grain hardness
<i>nahF</i>	NADH dehydrogenase	EST-clon 28-A10, (Ogihara et al. 2002)	cp (Ogihara et al. 2002)	Electron transport
<i>GPX</i>	glutathione peroxidase 1, cytosolic	AY364468	5A (Kocsy et al. 2004)	Antioxidative defence
<i>Lr10</i>	leaf rust resistance gene <i>Lr10</i>	(Feuillet et al. 2003)	IAS (Scherner et al. 2002)	Leaf rust resistance against Puccinia triticina
<i>RGA2</i>	leaf rust resistance gene analog for <i>Lr10</i>	(Feuillet et al. 2003)	IAS (Scherner et al. 2002)	Leaf rust resistance analog against Puccinia triticina
<i>Q</i>	Q-Locus	(Paris et al. 2003)	SAL (Paris et al. 2003)	Domestication, free-threshing
<i>VRN1</i>	Vernalization gene 1	(Yan et al. 2003)	SAL (Yan et al. 2003)	Vernalisation, regulation of flowering

Chr chromosomal position, uncertain chromosomal positions are indicated with an asterisk

cp chloroplast genome

EST expressed sequence tags from a einkorn grain cDNA library. Kilian B, unpublished.

Nm not mapped

Supplementary Table S4. Primer and PCR conditions

Symbol	bp	Primer Name	Primer sequence	PCR conditions			
				Anneal Temp	Anneal Time	Elong Time	Cycles
<i>BAMY1</i>	469	130A	CAA CTA TGT CCA AGT CTA CGT C	63.5	30	50	28
		130C	TGC CAC CGC ACT GGT GGA ATG				
<i>GAPDH</i>	561	462E	GTC CTG AGT ACG TTG TTG AG	60.5	40	50	28
		462F	GAC CAT CAA CAG TCT TCT GG				
<i>ACC1</i>	804	Ac17	AGG TTG AGC ATC CAG TCA CC	63.0	40	50	28
		AcZ3	GTT ATT GCT GCT CTA GAC ACT C				
<i>PGK1</i>	716	PK11	TCG TCC TAA GGG TGT TAC TCC TAA	61.0	40	50	29
		PK19	AGG GAT TCG ATA ACC CCA ATC				
<i>AGPL*</i>	1009	APz1	TGA CTT TGG GTC TGA AAT CCT C	60.5	40	70	30
		APz2	GTT CAT GTC GAT GAT GCA GTT G				
<i>CesA</i>	769	CE05	TGC ACC AAT CAA TCT CTC TGA C	61.0	40	50	28
		CE04	CCA CCA GGT TAA TCA CAA GGA C				
<i>6SFT</i>	874	FU16	ACC GAC TCC TTG AGT GCC AAC	65.0	30	55	29
		FU18	CCG GGT CTT ATC ATC CAA CAC T				
<i>BADH</i>	546	BA16	GAC TCT ATT TGG GTG CTT TTG G	64.0	30	40	31
		BA15	CTT CAC TAA CAA CTG GCC CAA G				
<i>PEPC</i>	794	PE08	GTG GTG GCA ACT GAA GAA TAT C	62.5	40	50	29
		PE09	CAG CTT CTG GGT CTC CTC ATA G				
<i>G6PDH</i>	749	G601	GCA GGG AAG AAA TGA GTT TGT C	62.0	40	50	29
		G602	GTG GGT GGT ATC CAG ATG TAA C				
<i>GPT</i>	673	GT08	CCA ATC AAC GGT CTA AAT CAG C	63.0	30	50	31
		GT14	ATA CAG GCA TCG GAA ATG ACT C				
<i>pinB</i>	598	pB01	AAC GCA CCA TTT CTG TTG G	62.0	30	50	33
		pB02	AGC CAC TAG GTA ATT TGC AGT C				
<i>ndhF</i>	719	nd01	GGA AAA AGG ATA CCC AAA GGA G	63.0	40	50	29
		nd02	ATT CGA CCT CCC CCT ACA TAT T				
<i>GPX</i>	664	GX03	ACT CCA ACT ACA CCG AGC TGA G	64.0	30	50	29
		GX12	ATA GCG GTC CAC AAC GTG AC				
<i>Lr10</i>	709	R103	CAA AAT GTG TAG ATC GGC AGA G	62.0	30	50	31
		R104	TGG CCC ATC CAT TTA CCA AG				
<i>RGA2</i>	600	R203	ACC TGG CTA GAT GTT GTG AAG C	63.5	40	50	29
		R204	AGG TAA CTT GAG GCA ACT GGA G				
<i>Q</i>	916	Q05	CGA CAT CAA CTT CAA TCT GAG C	62.0	30	50	31
		Q08	TCA ACT TCG CTG TCA AAG AGG				
<i>VRNI</i>	621	AE01	TAT AGG AAA CTG AAG GCG AAG G	63.0	40	50	29
		AE11	GCA GCA AGA ACG ATG TAA TGA G				

*additional sequencing primer: APz3 CAA AGT CAG ACA AGT GCA GG
APz4 CGC TTC CGG AGT TTA GGC GTG

bp	amplified fragment in base pairs
Anneal Temp	Annealing temperature
Anneal Time	Annealing time
Elong Time	Elongation time

Supplementary Table S5. GenBank accession numbers for einkorn haplotypes

Locus	Haplotype	Accession-Number	Number of lines carrying the haplotype
<i>BAMY1:</i>	Tm07-I	EF382866	54
	Tm04-II	EF382867	56
	Tm120-III	EF382868	33
	Tb1215-IV	EF382869	146
	Tb1027-V	EF382870	5
	Tb1008-VI	EF382871	36
	Tu1122-VII	EF382872	10
	Tu1504-VIII	EF382873	2
	Tu388-IX	EF382874	27
	Tb590-X	EF382875	59
	Tb1303-XI	EF382876	3
	Tm190-XII	EF382877	13
	Tb600-XIII	EF382878	4
	Tb1299-XIV	EF382879	2
<i>GAPDH:</i>	Tm109-I	EF382941	17
	Tb640-II	EF382942	371
	Tb736-III	EF382943	2
	Tb1291-VI	EF382944	22
	Tu1362-VII	EF382945	39
<i>ACCI:</i>	Tm209-I	DQ290259	42
	Tb1272-II	DQ290268	227
	Tb604-III	DQ290262	3
	Tb746-IV	DQ290267	1
	Tb1331-V	EF382965	128
	Tb1108-VI	DQ290261	2
<i>PGK1:</i>	Tb1292-VII	DQ290266	5
	Tu1556-IX	EF382966	39
	Tb585-I	DQ290658	228
	Tb766-II	DQ290660	6
	Tb1141-III	DQ290665	7
	Tm15-V	DQ290662	170
<i>AGPL:</i>	Tb751-VI	DQ290664	2
	Tu393-VIII	DQ290659	33
	Tu1455-IX	DQ290661	6
	Tb590-I	EF382891	60
	Tb1196-II	EF382907	23
	Tb1317-III	EF382904	5
	Tm1378-IV	EF382905	2
	Tm104-V	EF382889	125
	Tb1319-VI	EF382906	1
	Tb766-VII	EF382892	3
	Tb1037-VIII	EF382893	12
	Tb1106-IX	EF382894	17
	Tb1305-X	EF382895	7
	Tb583-XI	EF382896	102
	Tb779-XII	EF382897	2
	Tb46/2-XIII	EF382898	3
	Tu1548-XIV	EF382899	18
	Tu1404-XV	EF382900	13
	Tu1463-XVI	EF382901	6
	Tu1442-XVII	EF382902	2
	Tm508-XVIII	EF382890	38
	Tb1221-XIX	EF382903	7
<i>CesA:</i>	Tm14-I	EF382946	102
	Tb731-II	EF382947	283
	Tb1304-III	EF382948	6
	Tu388-IV	EF382949	28
	Tu1425-V	EF382950	7
	Tu394-VI	EF382951	4
	Tb755-VII	EF382952	21
<i>6SFT:</i>	Tb751-I	EF382908	109
	Tb14/1-II	EF382927	1
	Tm1331-III	EF382911	3

Tb625-IV	EF382912	13
Tb757-V	EF382910	217
Tm05-VI	EF382913	8
Tb753-VII	EF382909	11
Tu1396-VIII	EF382914	36
Tu393-IX	EF382915	2
Tb1301-X	EF382916	2
Tb597-XI	EF382917	5
Tb1150-XII	EF382918	11
Tb226-XIII	EF382919	2
Tb824-XIV	EF382920	4
Tb787-XV	EF382921	2
Tb1313-XVI	EF382922	2
Tb995-XVII	EF382923	14
Tb843-XVIII	EF382924	3
Tb1109-XIX	EF382925	2
Tb1289-XX	EF382926	1
 <i>BADH:</i>		
Tm04-I	EF382880	399
Tb1111-II	EF382882	3
Tb228-III	EF382883	4
Tu388-V	EF382884	23
Tb1291-VII	EF382885	2
Tu1425-VIII	EF382886	7
Tu1362-IX	EF382887	5
Tu393-X	EF382888	4
Tb22/2-XI	EF382881	4
 <i>PEPC:</i>		
Tb26-I	EF382953	408
Tb795-II	EF382954	5
Tu388-III	EF382955	39
 <i>G6PDH:</i>		
Tm04-I	DQ290381	371
Tb754-III	DQ290380	6
Tb226-IV	DQ290379	32
Tu388-V	DQ290382	39
 <i>GPT:</i>		
Tm04-I	DQ290496	430
Tu393-II	DQ290493	7
Tu1404-III	DQ290494	13
Tb1308-IV	DQ290495	2
 <i>pinB:</i>		
Tm259-I	EF382928	41
Tm476-III	EF382929	2
Tm07-IV	EF382930	10
Tb386-V	EF382931	16
Tb600-VI	EF382932	19
Tb1309-VII	EF382933	3
Tm15-VIII	EF382934	89
Tb585-X	EF382935	193
Tb649-XI	EF382936	9
Tu393-XII	EF382937	24
Tu388-XIII	EF382938	17
Tm508-XIV	EF382939	18
Tb1110-XVI	EF382940	8
 <i>ndhF:</i>		
Tm04-I	DQ290596	413
Tu388-II	DQ290597	39
 <i>GPX:</i>		
Tb1100-I	EF382956	238
Tb1308-II	EF382957	2
Tb909-III	EF382958	15
Tb751-IV	EF382959	76
Tb1089-V	EF382960	4
Tu1396-VI	EF382961	37
Tu1122-VII	EF382962	2
Tm435-VIII	EF382963	63
Tb22/2-XI	EF382964	11
 <i>Lr10:</i>		
Tu1425-I	EF382989	14
Tu122-II	DQ290915	13
Tb604-III	DQ290911	15
Tb1319-V	DQ290919	6
Tu1423-VI	DQ290909	9
Tm508-VIII	DQ290912	12
Tm1331-IX	EF382990	35

CHAPTER 7

Locus	Haplotype	Accession-Number	Number of lines carrying the haplotype
	Tm209-X	DQ290923	7
	Tb1239-XI	DQ290913	17
	Tb601-XII	DQ290908	5
	Tu1527-XIV	EF382991	5
	Tb1310-XV	EF382992	2
	Tu1122-XVI	EF382993	10
	Tu393-XVIII	EF382994	2
<i>RGA2:</i>	Tm14-I	EF382968	82
	Tb386-II	EF382969	56
	Tb1292-III	EF382970	4
	Tm69-IV	EF382971	5
	Tu388-VI	EF382972	14
	Tb784-VII	EF382973	24
	Tb1110-VIII	EF382974	41
	Tb1291-IX	EF382975	10
	Tm115-X	EF382976	3
	Tb1142-XI	EF382977	2
	Tm07-XII	EF382978	42
	Tb703-XIII	EF382979	14
	Tb751-XIV	EF382980	135
	Tb1314-XV	EF382982	1
	Tb1307-XVI	DQ290965	4
	Tb1677-XVII	EF382981	1
<i>Q:</i>	Tm04-I	DQ290774	87
	Tm1259-II	DQ290775	9
	Tb754-III	DQ290776	39
	Tb870-IV	DQ290777	8
	Tb386-V	DQ290778	197
	Tb862-VI	DQ290779	2
	Tb597-VII	DQ290780	51
	Tb585-VIII	DQ290781	12
	Tb1290-IX	DQ290782	5
	Tu1404-X	DQ290783	19
	Tu1504-XI	DQ290784	2
	Tu1425-XIII	DQ290786	16
	Tu1547-XIV	EF382967	2
<i>VRNI:</i>	Tb752-I	EF382983	333
	Tb226-III	DQ291018	2
	Tb1002-IV	DQ291022	2
	Tb682-V	DQ291021	38
	Tb751-VI	EF382984	23
	Tb760-VII	DQ291020	3
	Tu388-VIII	EF382988	39
	Tb50/1-IX	EF382985	2
	Tb56/1-X	EF382987	3
	Tb42/1-XI	EF382986	3

Note: Of 7831 sequences analyzed here, 7792 are original sequence data, 39 are retrieved from GenBank.

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Chapter 8

Natural variation and identification of microelements content in seeds of einkorn wheat (*Triticum monococcum*)

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Abstract

Micronutrient deficiencies in human beings are common problems, especially in developing world. Among the micronutrient deficiencies, zinc (Zn) and iron (Fe) deficiencies are particularly important affecting severely health of humans. 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 world. In the present study, the variation for seed content of micronutrients (Zn, Fe, Mn and Cu) in 54 accessions of einkorn wheat (*Triticum monococcum*) was tested. The accessions have been first grown under same field conditions in 2 locations in Turkey, and the seeds obtained from the field trials were analyzed for micronutrients. In addition, a mapping population with 168 recombinant inbred lines which were grown in 4 locations in Germany, Turkey and Italy has also been tested for the variation of micronutrients in seeds and analyzed for identification of QTLs associated with micronutrient content in seeds.

The results obtained showed existence of large genotypic variation in content of micronutrients. The contents of Zn and Fe among the 54 einkorn wheat accessions varied from 0.21 to 2.16 µg seed⁻¹ for Zn with an average of 1.19 µg seed⁻¹ and from 0.54 to 3.09 µg seed⁻¹ for Fe with an average of 1.15 µg seed⁻¹. There was a close positive relationship between seed contents of Fe and Zn. The genetic basis of this variation was elucidated by QTL analysis, using a mapping population comprising 168 recombinant inbred lines that was developed from a cross between 2 cultivated einkorn genotypes (e.g., ID-362 bread-making quality poor and ID-1331 bread-making quality good). From the parents ID-362 had always more Zn than the other parent in all four locations. The four locations presented different mean values, varying from 1.09 to 2.16 µg seed⁻¹ for Zn content, from 0.83 to 1.97 µg seed⁻¹ for Fe content, from 1.43 to 1.97 µg/seed⁻¹ for Mn content and from 0.14 and to 0.24 µg seed⁻¹ for Cu content. Pooling the results of the four trials, a major QTL, common to all four microelements and explaining from 10 to 30% of the variation (depending on the mineral assayed), was observed only on the chromosome 5, and not on the other chromosomes. The einkorn germplasm tested had a significant variation for micronutrients, especially Zn and this variation could be exploited in breeding programs. Chromosome 5 likely carries the genes affecting micronutrient accumulation in einkorn seeds.

Introduction

Currently, half of the world population suffers from micronutrient deficiencies, especially Fe and Zn. Zinc and Iron deficiencies cause very serious health problems such as impairments in the immune system, physical growth, mental and cognitive development and increases in anemia, morbidity and mortality (Welch and Graham 1999; Hotz and Brown 2004). As a main source of calorie intake, cereal-based foods are extensively consumed in the developing world. However, cereals are inherently very poor both in concentration and bioavailability of Zn and Fe in seeds. Welch and Graham (1999) reported that cereal grains are the primary source of Fe and Zn for people in developing countries; however, intakes do not satisfy their mineral requirements. Increasing the total amount and bioavailability of Zn and Fe in food crops is, therefore, a big challenge.

One major approach to minimize micronutrient deficiencies in human beings in developing countries is the selection and development of new plant genotypes with high grain density of micronutrients in edible

parts. Existence of large genetic variation for micronutrients in seeds is essential for a successful breeding program aiming at development of micronutrient-rich new plant genotypes. Several authors have reported a large genotypic variation for Zn and Fe in different cereal species (Peterson et al. 1986; Rengel et al. 1999; Graham et al. 1999; Cakmak et al. 2000). A number of recent studies deal with genetic variation for microelement content in seeds, such as in bean (Beebe et al. 2000), rice (Gregorio et al. 2000), wheat (Ortiz-Monasterio and Graham 2000; Cakmak et al. 2004) and maize (Banziger and Long 2000). In cultivated wheats, variation in seed Zn and Fe concentration is relatively small and seems to be not promising for a genetic improvement of wheat (Rengel et al. 1999; Cakmak et al. 2004). Compared to cultivated wheat cultivars, wild and primitive wheats, such as *Triticum monococcum*, *T. dicoccoides* and *T. dicoccum* were found to be much more promising genetic donors for micronutrients (Cakmak et al. 2000; Cakmak et al. 2004; Ortiz-Monasterio and Graham 2000). Among wild wheat germplasm, the wild emmer wheat, *T. dicoccoides*, showed the largest variation and the highest concentration of micronutrients, especially for Zn, and is considered a promising genetic source to improve Zn and Fe concentrations of wheat seeds (Cakmak et al. 2004). However, little is known for the diploid wheat *T. monococcum*. Einkorn wheat produces protein equal to durum when grown under adverse condition (Vallega 1979). In addition, the seed amino acid composition in einkorn is similar to those of other wheats, irrespective of a very large variation in total proteins (Acquistucci et al. 1995). *T. monococcum* was also found to contain high levels of both protein and carotenoids (Borghi et al. 1996). According to Borghi et al. (1996) *T. monococcum* genotypes contain nearly 7 times more carotenoids than cultivated wheat. It is important to study the genetic potential of *T. monococcum* and the mapping populations derived from *T. monococcum* for micronutrients and to characterize the localization of genes and QTLs involved in micronutrient accumulation in seeds.

The main objectives of this study were a) to determine the degree of genetic variability for micro-elements in einkorn wheat accessions; and b) to identify QTL associated with microelements content (particularly Zn and Fe) in einkorn wheat, using 168 recombinant inbred lines derived from a cross between ID 362 (poor breadmaking quality) and ID 1331 (good breadmaking quality)

Materials and Methods

In the present study, seeds of 54 accessions of einkorn (*T. monococcum*) were used for analysis of Zn, Fe, Mn and Cu. These accessions were kindly obtained from USDA. All lines were grown in 2003–2004 at Adana, Turkey, in two contrasting environments (upland and lowland conditions). The seeds obtained from the field trials were dehulled and analyzed for Zn, Fe, Mn and Cu by using inductively coupled plasma-atomic emission spectrometry (ICP-AES). Seed samples were digested by using a microwave digesting system and then subjected to ICP tests. The measurements were checked using the certified mineral nutrients values in durum wheat flour samples obtained from the National Institute of Standards and Technology. The reference materials used was the durum wheat flour (8436).

The Map

A mapping population has been used to study genetic variation for micronutrients and to identify QTLs which are associated with high micronutrient concentration in seeds. The original consensus map (fig. 1, Taenzler et al. 2002) was built from two populations of 117 and 168 F2 plants, respectively, from which F3 families were derived. Population 1 (117 progenies) was derived from a cross between ID 49, a wild einkorn line (*T. m. ssp. boeoticum*), and ID 69, a free-threshing, cultivated einkorn (*T. m. ssp. monococcum*

var. sinskajae). Population 2 (168 progenies) was derived from a cross between two cultivated einkorn lines with different breadmaking quality, ID 362 (poor quality) and ID 1331 (good quality). The integrated map, based on the data sets for both populations and including 477 markers (32 RFLPs, 438 AFLPs, one morphological and six storage-proteins), was assembled using JoinMap version 2.0 (Stam and Van Ooijen 1995). Its total length is of 856 cM, with an average distance of 1.8 cM between markers.

Microelements Content

To assess microelements content, F3-derived families of Population 2 were grown in Sant'Angelo Lodigiano (Italy) in 1998 (S98) and 2004 (S04), in Cologne (Germany) in 2003 (K04) and in Adana (Turkey) in 2004 (A04), in 10 m² plots, following the agronomic practices described by Castagna et al. (1995). After harvest, the seeds were manually dehulled and microelements content assessed as above described. Data obtained for F3-derived families were taken as indicators of values for individual F2 plants.

QTL Analysis

To localize the QTLs responsible for microelements content, the chromosome marker order determined by JoinMap was transferred to the computer program PLABQTL (Utz and Melchinger 1996), together with laboratory data (Fe, Zn, Mn and Cu content) of Population 2. The numbers of markers mapped in Population 2 and considered in our QTL analysis were 36, 28, 33, 18, 37, 26 and 13, respectively, for linkage groups 1 to 7 (data not shown). The allelic average substitution value of the chromosome fragment hosting the microelement-related gene was determined by halving the differences between the genotypic values of the two homozygotic classes.

Results

Genetic variation for microelements between einkorn accessions

The analysis of microelements concentration and content in seeds of einkorn accessions grown in Adana, in two environments, are presented in table 1. Clear variation was observed in seed micronutrient concentrations among the accessions. Zinc content of the seeds varied from 0.21 to 2.16 µg seed⁻¹, with an average of 1.21 µg seed⁻¹ and Fe content varied from 0.54 to 3.09 µg seed⁻¹, with an average of 1.27 µg seed⁻¹.

Table 1. Concentration and content of Zn, Fe, Mn and Cu in seeds of 54 *Triticum monococcum* accessions grown in two different places

Locations	Concentration (mg kg ⁻¹ dry wt)							
	Zn		Fe		Mn		Cu	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Upland	51	36–76	43	32–61	42	26–60	6.6	4.1–10
Lowland	59	44–84	51	35–85	56	31–92	6.2	3.9–9.1

Locations	Content g seed ⁻¹							
	Zn		Fe		Mn		Cu	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Upland	1.21	0.37–2.07	1.02	0.54–2.07	1.01	0.53–2.08	0.16	0.10–0.23
Lowland	1.17	0.21–2.16	1.27	0.62–3.09	1.32	0.54–2.23	0.41	0.10–2.56

A similar variation was also found with Mn, but in the case of Cu the genetic variation was lesser. There was a significant ($P \leq 0.05$) positive correlation between microelements in two locations, most noticeably for Zn, which correlated with Fe, Mn and Cu (data not shown). Similar results were reported by Cakmak et al. (2004) for Zn and Fe. The correlation between Fe and Zn in grain was also reported by Peterson et al. (1986) and Graham et al. (1999). This may point to common genetic mechanisms controlling Zn and Fe uptake and seed deposition. Correlations among microelements indicate that the improvement of one micronutrient (e.g. Zn) may simultaneously improve the content of other micronutrients (e.g. Fe). The variation for Zn, Fe, Mn and Cu content in seed was much greater when compared to the variation found for the concentration (table 1). These results suggest that I) ample genetic variation is detected in the progeny of crosses if the parents have different microelements contents; and II) it is possible to develop new wheat cultivars with higher Zn and Fe content.

Mapping Population

In the ID 362 x ID 1331 mapping population, the content of four microelements was determined in four different locations: S98, K03, S04 and A04 (see Material and Methods). The parent ID 362 always showed higher content of microelements than the ID 1331 (table 2); the average lowest and highest values over the locations were 2.06 vs 3.12 for Zn, 1.63 vs 1.80 for Fe, 1.76 vs 2.06 for Mn and 0.12 vs 0.18 for Cu. The four locations differed in mean values of micronutrients, varying from 1.09 (A04) to 2.16 (S04) for Zn content, from 0.83 (A04) to 1.97 (K03) for Fe content, from 1.43 (K03) to 1.97 (S98) for Mn content and from 0.14 (S98 and A04) to 0.24 (S04) for Cu content. Among progenies within locations, the values between samples

Table 2. Average values (\pm s.e.) recorded for Population 2 (parents and F3-derived progenies) for microelements content. For F3 progenies, the field of variation covered by single progenies is also reported

Micro-element	Genotype	Location				
		S98	K03	S04	A04	Average
Zn	ID 362	2.91 \pm 0.04	3.50 \pm 0.00	2.95 \pm 0.18	-*	3.12 \pm 0.19
	ID 1331	2.40 \pm 0.11	2.04 \pm 0.34	1.74 \pm 0.07	-	2.06 \pm 0.19
	progenies	1.98 \pm 0.03	1.50 \pm 0.03	2.16 \pm 0.03	1.09 \pm 0.02	1.70 \pm 0.02
	range	1.29 - 3.40	0.96 - 2.85	1.26 - 3.68	0.49 - 1.72	1.15 - 2.33
Fe	ID 362	1.89 \pm 0.03	2.34 \pm 0.44	1.18 \pm 0.07	-	1.80 \pm 0.34
	ID 1331	1.78 \pm 0.17	2.03 \pm 0.69	1.08 \pm 0.03	-	1.63 \pm 0.28
	progenies	1.46 \pm 0.02	1.97 \pm 0.04	1.15 \pm 0.02	0.83 \pm 0.02	1.36 \pm 0.02
	range	0.92 - 4.63	0.99 - 4.59	0.71 - 1.99	0.33 - 1.31	0.96 - 1.96
Mn	ID 362	2.65 \pm 0.07	1.71 \pm 0.36	1.81 \pm 0.11	-	2.06 \pm 0.30
	ID 1331	2.30 \pm 0.07	1.60 \pm 0.15	1.39 \pm 0.02	-	1.76 \pm 0.28
	progenies	1.98 \pm 0.03	1.43 \pm 0.03	1.47 \pm 0.02	1.70 \pm 0.05	1.64 \pm 0.02
	range	1.28 - 2.91	0.81 - 2.50	0.78 - 2.22	0.62 - 3.52	1.16 - 2.40
Cu	ID 362	0.06 \pm 0.00	0.18 \pm 0.02	0.31 \pm 0.02	-	0.18 \pm 0.07
	ID 1331	0.05 \pm 0.01	0.12 \pm 0.04	0.20 \pm 0.01	-	0.12 \pm 0.04
	progenies	0.14 \pm 0.03	0.15 \pm 0.00	0.24 \pm 0.00	0.14 \pm 0.00	0.17 \pm 0.00
	range	0.04 - 0.21	0.01 - 0.27	0.16 - 0.38	0.06 - 0.26	0.11 - 0.24

* No parents analyzed

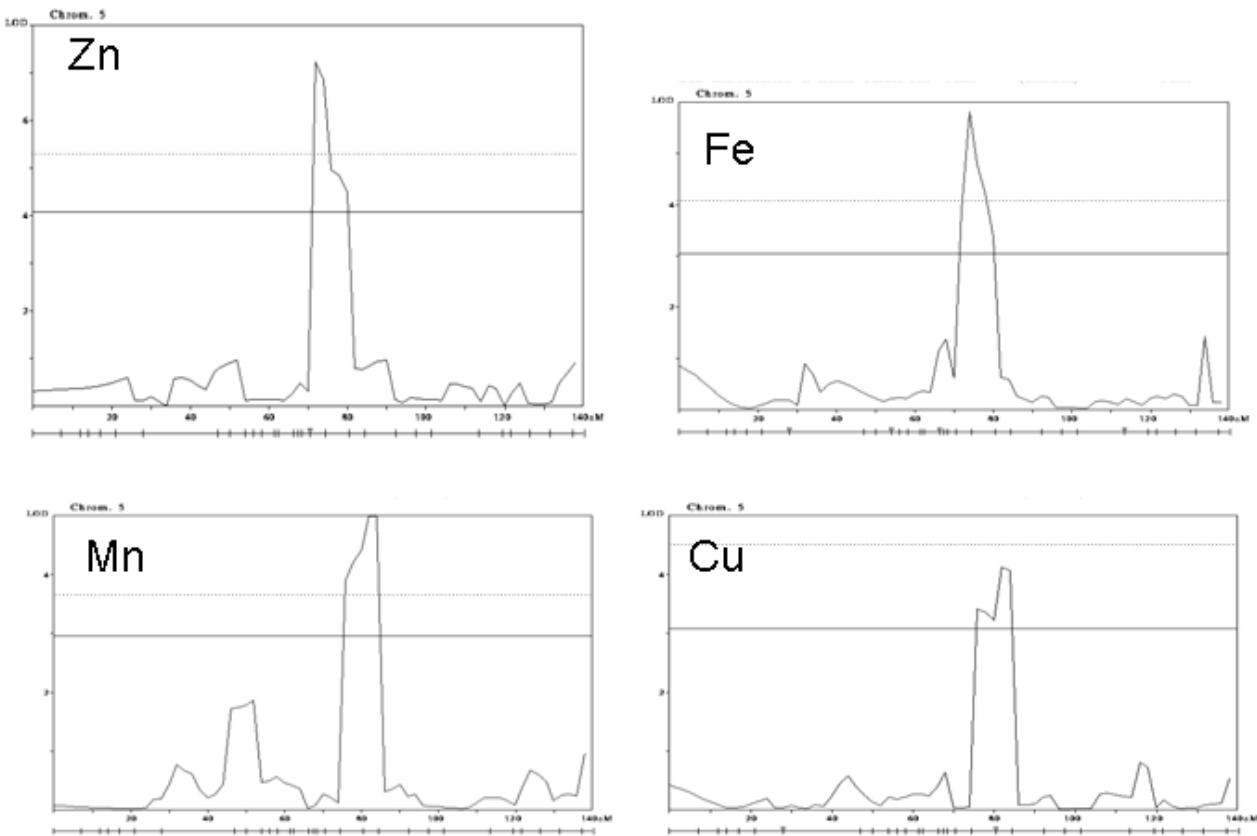


Fig. 1. - Localization on einkorn chromosome 5 of QTLs controlling Zn, Fe, Mn and Cu content. The analyses are based on the average contents of four locations. The LOD thresholds corresponding to $P \leq 0.05$ (solid lines) are 4.09, 3.04, 2.96 and 3.08, respectively, while the LOD thresholds corresponding to $P \leq 0.01$ (dotted lines) are 5.22, 4.10, 3.76 and 4.44, respectively.

with low and high microelements content varied 2– to 5-fold; averaged over location, the progenies with high microelements content showed values double than those with low content. The frequency distribution of Zn, Fe, Mn and Cu level showed considerable transgression in both directions for all microelements (data not shown). This suggests that both accessions carry genes with alleles contributing to an increased content for all microelements tested.

QTL Analysis

For all the traits considered, two LOD score thresholds were computed, the first corresponding to a significance level of $P \leq 0.05$ and varying between 2.96 and 4.08, and the second corresponding to a significance level of $P \leq 0.01$ and varying between 3.76 and 5.22, depending on the microelement considered. The analyses revealed a major QTL on chromosome 5, insisting in the same interval and present in two environments (S98 and K03) for Zn and Mn, and only in K03 for Fe. For Zn and Mn content, second QTL was detected on chromosome 1 in one location (K03). No QTLs were evident for Cu content, even though smaller peaks were present in the same chromosome 5 position of the other microelements. The analyses carried out by pooling the data of the four locations confirmed the existence of a strong QTL ($P \leq 0.05$) between 71 cM and 86 cM from the tip of the short arm of chromosome 5 that is associated with Zn, Fe, Mn and Cu content. Three out of four QTLs (for Zn, Fe and Mn) were significant also at LOD scores corresponding to $P \leq 0.01$ (fig. 1). The substitution value of the allele originating from ID 362 varied between +0.30 (for Cu) and +0.42 (for Zn), indicating that the allelic segment encompassing the region of the QTL in ID 362 induces an increase of 0.30 to 0.42 units (depending on the microelement) compared with the

same allelic fragment of ID 1331. Minor dominance effects (+0.15 and +0.12) of complementary sign to the additive effect were observed in the case of Zn and Fe, respectively. The results obtained suggest that the *T. monococcum* is a promising genetic resource for working genetic variation and identification of genes for micronutrients; especially Zn. Studies are on-going to collect more information on the localization of genes affecting content of micronutrients (especially Zn) in different genetic stocks derived from *T. monococcum*.

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Chapter 9

Haplotype structure at seven barley genes: relevance to gene pool bottlenecks, phylogeny of ear type and site of barley domestication

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Abstract

Archaeological remains indicate that the origin of western agriculture occurred in a brief period about 10,500 years ago in a region of the Middle East known as the Fertile Crescent, where the wild progenitors of several key agricultural cereal species are endemic. Domestication entailed the appearance of agronomic traits such as seed size and threshability. For a representative sample of 20 domesticated barley (*Hordeum vulgare*) lines, including 13 two-rowed and 7 six-rowed varieties, we determined the haplotypes at seven loci—*Adh2*, *Adh3*, *Amy1*, *Dhn9*, *GAPDH*, *PEPC* and *WAXY* encompassing 5,616 bases per line—and compared them to the haplotypes at the same loci for 25 wild forms (*Hordeum spontaneum*) collected within and outside the Fertile Crescent. In comparisons of wild versus domesticated barley, the number of haplotypes (70 vs. 17), average nucleotide diversity, π , (0.0077 vs. 0.0028), and Watterson's theta at silent sites (0.0104 vs. 0.0028) was reduced in domesticated lines. Two loci, *Amy1* and *PEPC*, were monomorphic in domesticated lines; *Amy1* and *GAPDH* produced significant values of Tajima's D. 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, 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. Phylogenetic networks data uncover distinct wild and domesticated barley genotypes and suggest that barley may have been domesticated in the Jordan valley. Because, based on AFLP data, the domesticated Turkish cultivars had a genetic basis as large as that present in large germplasm collections, all comparisons provided in this paper are of general value more than being restricted to the Turkish barley germplasm.

Introduction

The domestication of grasses began during “the Neolithic revolution”, about 12,000 years before present (BP), when humans living as hunter-gatherers became sedentary food producers (Diamond 1997; Salamini et al. 2002). In genetic terms, grass domestication involved human counterselection against unfavorable alleles at loci governing flowering time, rachis brittleness, naked seeds, and seed size, accompanied by the accumulation of small genetic effects at quantitative trait loci (QTLs) that, collectively, confer yield increase, reduction in plant height, changes in tillering, inflorescence, and plant architecture (Salamini et al. 2002). Domestication traits were probably selected as a grass-specific set (Buckler et al. 2001), thus allowing a genetically “convergent” domestication across grasses, as demonstrated for maize, rice and sorghum (Paterson et al. 1995). The conversion from brittle to non-brittle rachis, the transition from distichous to polystichous spike, and the appearance of the naked caryopsis (nude) character (Søgaard and von Wettstein-Knowles 1987; Harlan 1976) were the main genetic and morphological events that accompanied the development of domesticated barley, *Hordeum vulgare*, from its wild progenitor *Hordeum spontaneum*. The domestication of barley is thought to have occurred in the Fertile Crescent (Badr et al. 2000; Salamini et al. 2002; Morrell et al. 2003) although varieties with naked seeds appear quite early in the Himalayan region, probably as the result of human dispersal and introgression (Badr et al. 2000).

Considerable allelic and haplotype diversity is found among wild barley populations (Nevo et al. 1979, 1986a, b; Snow and Brody 1984; Jana et al. 1987; Chalmers et al. 1992; Dawson et al. 1993; Badr et al. 2000; Lin et al. 2001, 2002; Morrell et al. 2003, 2005). Evidence favoring a monophyletic, or possibly diphyletic, domestication of barley in the Jordan valley (Badr et al. 2000; Salamini et al. 2004) would predict a reduction

of nucleotide diversity in alleles found among gene pools of domesticated versus wild *Hordeum* accessions in the wake of domestication bottlenecks. Reduced polymorphism following domestication effect can easily be misidentified as a signature of selection (Tenaillon et al. 2004; Wright and Gaut 2005; Wright et al. 2005). Domestication thus involves bottlenecks and the fixation of particular allele combinations during the initial domestication process, but is followed by the further reduction of variability at linked loci that have been selected by breeders since the domestication process. This reduction is a function of the rate of recombination between the selected sites and the linked loci surveyed. This hitchhiking effect can be detected as a skew in frequencies of molecular markers (Vigouroux et al. 2002) when compared to frequencies expected under an equilibrium-neutral model.

Only a few hundred effective meiotic cycles (those resulting from natural hybridization events or intentionally carried out by plant breeders) have occurred during the roughly 10,000 years endured by cereal germplasm in the domesticated condition (Paterson 2002). Accordingly, short chromosomal regions may exist in linkage disequilibrium (Paterson 2002; Rafalski 2002; Morgante and Salamini 2003), indicating that mutant alleles with significant effects on phenotypic traits may have been quickly fixed at several loci both early in the domestication process and during intentional breeding. In such a situation, small DNA regions flanking domestication-related or breeding-related loci are characterized by low levels of diversity (linkage drag). In a gene pool, the existence of domestication and breeding-related effects on the extent of natural variation can be detected by SNP loci, which permit assessment of haplotype diversity at specific loci (Schneider et al. 2001). Here we examine nucleotide diversity and haplotype combinations at seven loci in domesticated barley in comparison to that in *H. spontaneum*, the wild progenitor species.

Methods

Plant material

The correct taxonomical terminology for domesticated and wild barleys is *H. vulgare* subsp. *vulgare* and *H. vulgare* ssp. *spontaneum*, respectively. However, in all recent papers on this subject as well as in the reference book by Zohary and Hopf (2000), the wild is always named as *H. spontaneum*; in this article, we have followed the last taxonomical indication.

The plant material used in this study is listed in table 1. The 20 domesticated (D) lines represent barley varieties currently cultivated in Turkey, covering a long period of Turkish plant breeding. They were selected among 33 lines available and were chosen on the basis of maximum genetic distance to one another while also considering their morphological variation (see Results and Discussion). The 25 *H. spontaneum* lines (W) were those considered by Lin et al. (2001) and reported to span the native range of the wild species, including the Jordan valley, the putative site of barley domestication (Badr et al. 2000). Molecular variation found in the D lines, based on AFLP markers, was compared to that present in three groups of domesticated lines: two (20 lines each) were from the 67 lines cited in Castiglioni et al. (1998) and considered by Badr et al. (2000); the third group included the following 21 cultivars, representing a southern Europe gene pool of barley: Alexis, Angora, Apex, Arco, Aura, Betzes, Carina, Cherie, Express, Gitane, Jador, Magda, Mirko, Nudinka, Nure, Onice, Prisma, Proctor, Rebelle, Trebbia and Tremois.

The extent of phenotypic variation across D varieties was evaluated by an experiment carried out in two locations (upland and lowland conditions) in the Adana area (Mediterranean region, 37°21' N and 35°10' E), during the 2003–2004 growing season and under rainfed conditions. Each line was grown in 1 m row, in a randomized complete block design with three replications. All traits were recorded on ten individual plants.

CHAPTER 9

Table 1. Barley lines investigated in the present study

Line no.	Domesticated varieties	Breeding Institute	Year released	Use and rows in ear	Origin
3	Tokak 157/37	FCCRI-A	1937	F 2	Turkish land race
4	Kral 97	BDIWCR-K	1997	F 6	Land race
5	Avcı 2002	FCCRI-A	2002	F 6	Complex cross
6	Yesilköy 387	-	-	F 6	From Zogen 160, landrace from Kirklarhi
7	Aydahanim	FCCRI-A	2002	M 2	Cross of Omega x Tarm92
8	Hamidiye 85	AARI-E	1985	F 2	Tokak mutant
11	Cetin 2000	FCCRI-A	2000	F 6	Line 4875 from Iran
13	Zafer 160	FCCRI-A	-	F 6	Local land race
15	Cumra 2001	AEBMC-K	2001	M 2	Tokak mutant
16	Angora	ABMSIC-K	1999	M 2	Complex cross involving 6 lines
17	Erginel 90	AARI-E	1990	F 6	Cross of Escourgen x Hop21H (France)
20	Karatay 94	BDIWCR-K	1994	MF 2	Complex cross involving 5 lines
21	Tarm 92	FCCRI-A	1992	MF 2	Land race
23	Yesevi 93	FCCRI-A	1993	F 2	Land race
24	Kalayci 97	AARI-E	1997	F 2	Cross Erginel x Tokak
26	Efes 1	ABMSIC-K	-	ND 2	Unknown pedigree
27	Sladoran	TARI-E	1998	M 2	Introduction from Yugoslavia
30	Sahin 91	SAARI-D	1991	F 2	Unknown pedigree
31	Aday 4	-	-	ND 6	Unknown pedigree
33	Balkan 96	TARI-E	1996	M 2	Unknown pedigree

Line no.	Wild varieties ^a	PI no. ^b	Country of origin	Geographical region	
34	2	212305	Afghanistan	E	
35	3	212306	Afghanistan	E	
36	4	219796	Iraq	Z	
37	6	220523	Afghanistan	E	
38	9	236388	Syria	W	
39	10	253933	Iraq	Z	
40	11	254894	Iraq	Z	
41	12	268242	Iran	Z	
42	13	293402	Turkmenistan	E	
43	16	293409	Turkmenistan	E	
44	17	293411	Tajikistan	E	
45	21	296926	Israel	W	
46	22	366446	Afghanistan	E	
47	24	401370	Iran	E	
48	25	401371	Iran	Z	
49	27	406276	Israel	W	
50	28	420911	Jordan	W	
51	30	420913	Jordan	W	
52	32	420916	Jordan	W	
53	35	466460	Israel	W	
54	36	531851	Israel	W	
55	38	531853	Israel	W	
56	39	531857	Israel	W	
57	43	559556	Turkey	Z	
58	44	560559	Turkey	Z	

Line number used in this study

More details in Supplementary table 1 (Supplementary Material online)

Abbreviations are FCCRI-A Field Crops Central Research Institute, Ankara; BDIWCRI-K Bahri Dagdas International Winter Cereals Research Institute, Konya; AARI-E Anatolian Agricultural Research Institute, Eskisehir; AEBMC-K Anatolian Efes Beer and Malt Company, Konya; ABMSIC-K Anatolian Beer Malt and Southearn Industry Company, Konya; TARI-E Thrace Agricultural Research Institute, Edirne; SAARI-D Southeastern Anatolian Agricultural Research Institute, Diyarbakir; F feed; M malting; ND not described; E Eastern Fertile Crescent; W Western Fertile Crescent; Z Zagros (Morrell et al. 2003)

^aLine numbers as listed in the PNAS Supporting Information to Lin et al. (2001) ^bPlant introduction no.

Table 2. Barley genes and conditions used to amplify them in 20 domesticated barley varieties

Gene	Symbol	Chromosomal location	Accession numbers ^a	bp	Primer combination ^b	Annealing temperature (°C)	Elongation time (s)
Alcohol dehydrogenase 2	<i>Adh2</i>	4H	AY184931-955	837	B104-B106	61°C	50
Alcohol dehydrogenase 3	<i>Adh3</i>	7H	AF326691-715	825	B201-B202	61°C	50
Alpha-amylase 1	<i>Amy1</i>	6H	AY349195-219	663	B306-B307	62°C	50
Dehydrin 9	<i>Dhn9</i>	5H	AY349247-271	753	B503-B504	60.5°C	50
Glyceraldehyde-3-phosphate DH	<i>GAPDH</i>	6H	AY349298-322	765	B604-B605	61°C	50
Phosphoenolpyruvate carboxylase	<i>PEPC</i>	Nm	AY349272-297	945	B704-B705	60 °C	65
Granule bound starch synthase	<i>Waxy</i>	7H	AY349323-349	828	B806-B807	64.5°C	50

The published sequence for each gene and start-end positions for the amplified fragments in brackets are: (*Adh1*) AY184953 (1121-1957); (*Adh3*) AF326715 (109-923); (*Amy1*) AY349219 (86-748); (*Dhn9*) AY349270 (54-800); (*GAPDH*) AY349294 (197-960); (*PEPC*) AY349320 (77-1021); (*Waxy*) AY349344 (327-1151). Sequence data have been deposited in GenBank Data library under accession nos DQ195928 to DQ196067.

Nm; not mapped; Bp, base pairs amplified

^aAs listed in Lin et al. (2001); Lin et al. (2002); Morrell et al. (2003).

^b See Supplementary table 2 (Supplementary Material online).

Extraction of genomic DNA, generation of PCR primers and PCR amplification

Genomic DNA was isolated from silica-dried single leaves of each line with the Qiagen DNeasy Plant Mini Kit (Qiagen, Hilden, Germany), according to the manufacturers instructions. The Primer3 online software (primer3_www.cgi v 0.2, Whitehead Institute for Biomedical Research, Cambridge, UK) (Rozen and Skaletsky 2000) was used to design primers from published DNA sequences. Oligonucleotides were purchased from OPERON Biotechnologies (Cologne, Germany); their sequences are available in Supplementary table 2.

DNA amplifications were performed in a 25 µl volume. The reaction mix contained about 100 ng of genomic DNA, 0.4 µM of each primer, 125 µM of each dNTP (AB gene, Surrey, UK), 3 mM MgCl₂, 4% DMSO and 1 unit Taq DNA polymerase. The reactions were incubated in a PTC-225 Tetrad Thermal Cycler (MJ Research) with the following cycling conditions: 94°C for 3 min, 29–31 cycles of 30 s at 94°C, 40 s at 60.5–64°C, 50–65 s at 72 °C (depending on the gene, see table 1) followed by a final extension step of 6 min at 72°C. PCR products were separated by agarose gel electrophoresis and recorded as presence (1) or absence (0) of the amplified fragment.

Pre-screening for polymorphisms by non-denaturing gel electrophoresis

PCR products were digested, denatured for 3 min at 94°C, and characterized by SSCP-analysis, as described by Schneider et al. (1999, 2001). Electrophoresis of SSCP-gels (28.5 cm×25 cm×0.5 mm) was performed at room temperature with a constant power (1.0 W) for 12–16 h, the DNA fragments were visualized by silver staining.

Purification and sequencing of PCR products

Selected lines, representative of each haplotype for each locus, were selected based on SSCP-analysis. The corresponding PCR products were purified by ExoSAP-IT enzyme mixture (USB, Cleveland, USA) according to the protocol provided, and were sequenced directly on both strands on an Applied Biosystems (Weiterstadt, Germany) ABI Prism 3730xL sequencer using BigDye terminators. The amplification conditions for the seven genes in the domesticated barley lines are listed in table 2. Published sequence data for the seven loci from 25 wild barley lines (*H. spontaneum* C. Koch) were obtained from GenBank. The definition

Table 3. Interval of variation in two contrasting environments for spike and plant traits and for AFLP molecular markers in 20 domesticated barley varieties considered in this paper, as well as in 21 varieties from a Southern Europe gene pool. Fingerprints of Turkish domesticated lines were compared to those of the Southern Europe gene pool and to those of two groups of barley varieties studied by Badr et al. (2000)

Trait	Two-rowed (20 varieties)	Six-rowed (20 varieties)	% of polymorphic AFLP bands ^b	
AFLP primer combination	This paper		Badr et al. ^a	
	Turkish gene pool	Southern Europe gene pool	First group	Second group
1	23.7	44.4	44.8	45.8
2	76.0	49.6	50.0	50.5
3	49.1	47.5	57.7	53.1
4	38.7	48.5	46.1	51.3
5	45.2	53.0	51.9	50.0
6	3.1	-	41.6	48.7
7	43.5	-	52.5	53.3
All	44.5	48.6	49.2	50.5

^a Two groups of 20 varieties were chosen at random among the 57 considered by Badr et al. (2000).

^b Primer combinations listed (1 to 7) were respectively E36M40, E37M34, E37M32, E37M40, E37M45, E40M42 and E40M44 for the lines studied in this paper (Turkish and Southern Europe gene pools), and E36M40, E37M38, E41M40, E41M33, E36M44, E37M33 and E36M36 for the experiment of Badr et al. (2000).

of the molecular state for each haplotype of each gene sequenced was supported by multiple sequencings of the same haplotype from different genotypes.

AFLP genotype fingerprinting

The AFLP procedure of Zabeau and Vos (1993) was adopted. A total of seven primer combinations (table 3, note 1) were used to amplify *Eco*RI- and *Mse*I- digested DNA. Autoradiographs were scored for presence versus absence of polymorphic amplified DNA fragments.

SNP-detection

DNA sequences were processed with AB DNA Sequencing Analysis Software 5.1.1 (Data Collection Software version 2.0) and later manually edited by BioEdit version 7.0.1 (Hall 1999). Sequence alignments were generated in BioEdit, and the allelic haplotypes were defined.

Data analysis and statistics

Nucleotide diversity π (Nei 1987), Tajima's D (Tajima 1989), and Watterson's theta (Θ_w) were calculated by DNAsP v4.00 (Rozas 2003). Exon and intron sequence positions were derived from published data of *H. spontaneum* (Lin et al. 2001; Morrell et al. 2003). DNA sequences of the seven genes for each of the 20 domesticated varieties and of the 25 wild lines were analyzed both individually and as a concatenated data set with a total length of 5,616 bp. Neighbor-Net (NNet) planar graphs (Bryant and Moulton 2004) were constructed from the proportion of nucleotide differences between sequences, which was below 0.04 in all comparisons (fig. 1A). The distinct advantage of NNet for these data lies in its ability to uncover hybridization-like events, which may occur and which go undetected or are forced to signal-averaging in bifurcating trees (Bryant and Moulton 2004).

Maximum likelihood trees (see Supplementary fig. 1, Supplementary Material online) were computed with IQPNNI v2.6 (Vinh and von Haeseler 2004) for the concatenated data, stopping at the best tree with a confidence of 95%. For each IQPNNI run the default parameters were chosen, except for the concatenated sequences with a minimum number of 10,000 iterations.

To process the data presented in fig. 2, a matrix was created of one row for each individual line and one column for each of two possible alleles at each locus into which the major haplotypes (or AFLP data) were written, coded as single ASCII characters each. The Hamming distance (p-distance) between individual lines provides the measure of genetic identity. Individual lines that have the same collection of haplotypes are scored as identical ($P=0$), those differing at two alleles (of either one or two loci) are more different than those differing at one, and so forth, while those pairs sharing no haplotypes in common assume the maximum distance ($P=1$). This scores all differences between major haplotypes with equal weight, regardless of whether the haplotypes differ by 2 or by 20 nucleotides. NNet (Bryant and Moulton 2004) as implemented in SplitsTree 4 (Huson 1998) was used to process the p-distance data, to uncover shared similarities.

Also AFLP data from the seven primer combinations were concatenated to build a binary sequence (presence vs. absence of a band) for each of 20 domesticated variety (fig. 2A). The phylogenetic tree was reconstructed with Tree-puzzle v5.26 (Schmidt et al. 2002) using 10,000 iterations, the two-state substitution model (Felsenstein 1981), assuming a uniform rate heterogeneity, and default settings except the parameter estimation, which was calculated.

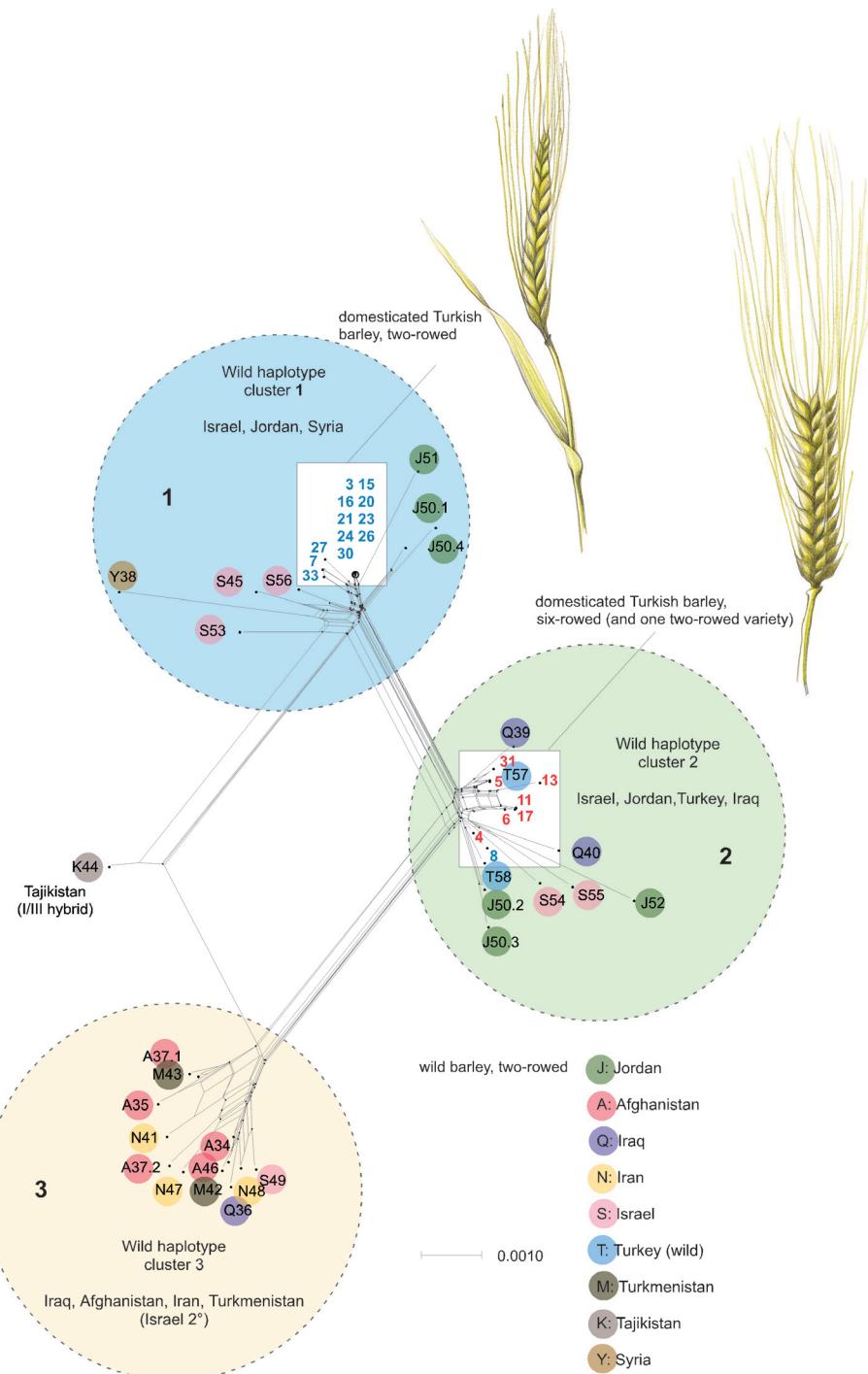
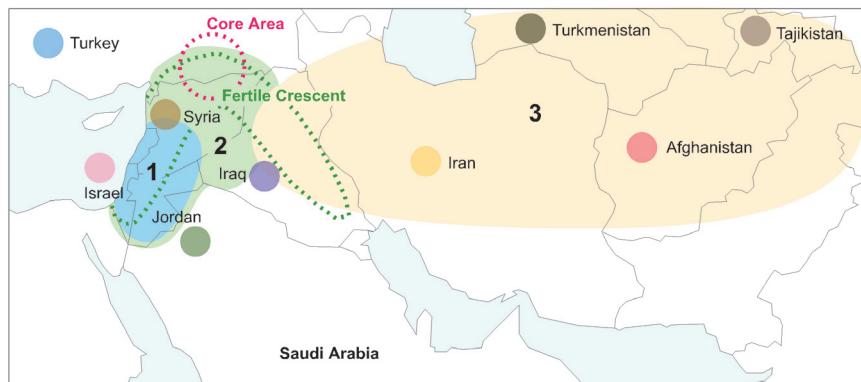
Results and discussion

The domesticated barley gene pool

A representative sample of Turkish barley varieties bred during the last 30 years was investigated as the domesticated (D) gene pool. The reason to focus on Turkish varieties stems from the considerations that Turkey includes part of the primary habitats of *H. spontaneum* and shares with the Fertile Crescent the same climatic conditions. Thus, the possibility that allelic frequencies in wild and domesticated gene pools were significantly and differentially modified by environmental factors is minimized.

Out of the 33 varieties listed in the Turkish register of barley varieties, 20 were considered based on their AFLP genetic distances (data not shown). Thus, in the D group only the varieties showing the widest genetic distance were included. Care was also taken to sample representatives of two- and six-rowed varieties, which among European varieties are frequently reported to have different genetic backgrounds.

To assess to which extent the Turkish D gene pool was representative of worldwide existing D pools, two approaches were followed. In the first, both two-rowed and six-rowed varieties were grown in replicated trials, and their morphological traits were recorded. The interval of variation for five such traits within two-

A**B**

and six-rowed varieties is present in table 3 (top part), pointing to the existence of significant phenotypical differences among genotypes. In the second approach, AFLP fingerprinting data of the 20 selected Turkish varieties were compared to the data recorded by Badr et al. (2000) for a wide spectrum of domesticated barley varieties. Badr et al. (2000) considered 57 out of 67 domesticated accessions described by Castiglioni et al. (1998). Their 67 genotypes were from a collection of 5,842 lines and were characterized by large differences in ear, grain and plant characters. The lines were landraces or old varieties cultivated in the Himalayan region, India, Yemen, Pakistan, Afghanistan, Turkestan, central Asia, Balkans, southern Europe, northern Europe, Ethiopia and Central Africa, America and Australia. The AFLP fingerprinting results (bottom part of table 3) indicate the percentage of polymorphic bands (295 loci) recorded for each of 7 AFLP primer combinations tested in the 20 Turkish D varieties, compared to similar data from two groups of 20 genotypes, chosen at random among those considered by Badr et al. (2000). The average proportion of polymorphic bands - 44.5% for the Turkish lines versus 49.2 and 50.5% for the two groups of 20 lines from Badr et al. (2000) - indicates that in terms of genetic variability, the 20 domesticated lines studied are a representative sample of the domesticated germplasm available worldwide. To reinforce further this conclusion, we have introduced AFLP data from the AFLP fingerprints (5 primer combinations) of 21 domesticated lines representative of a southern Europe gene pool. The proportion of polymorphic bands was, in this case, 48.6%. The conclusion on the domesticated gene pool sampled in Turkey and studied in this paper is that its interval of molecular variation, as measured by AFLP, is in the range of those typical of large collections of barley, or of a more western varietal gene pool. This provides evidence that the comparison between wild and domesticated lines presented in this paper has a general value, more than being only restricted to the Turkish domesticated germplasm.

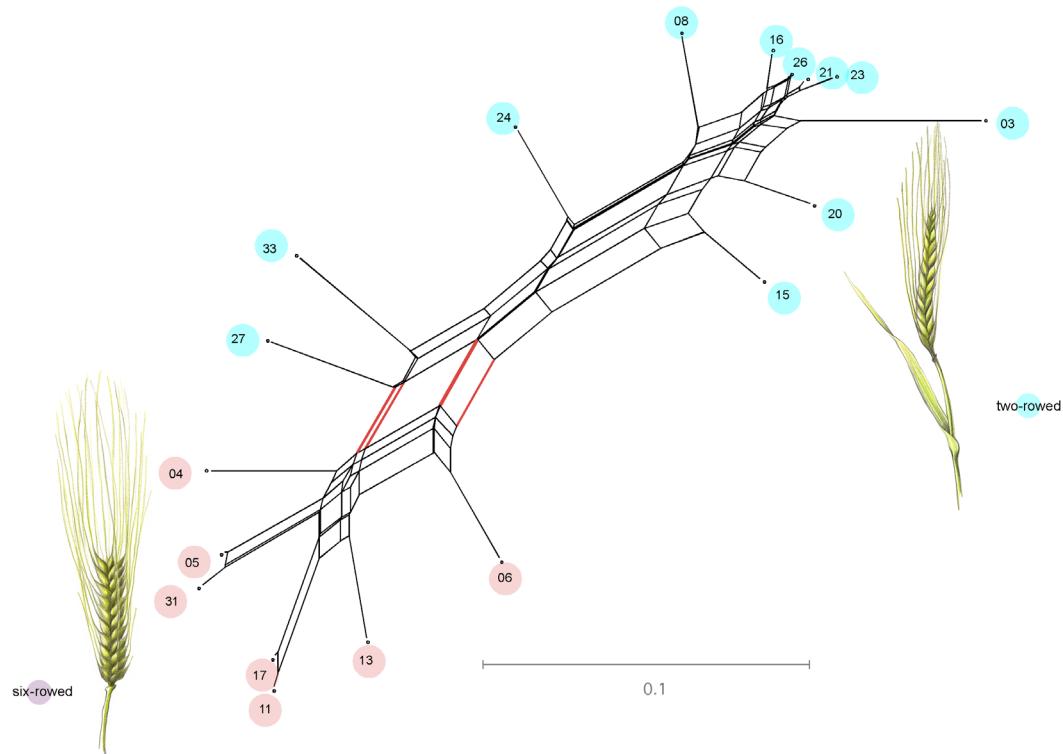
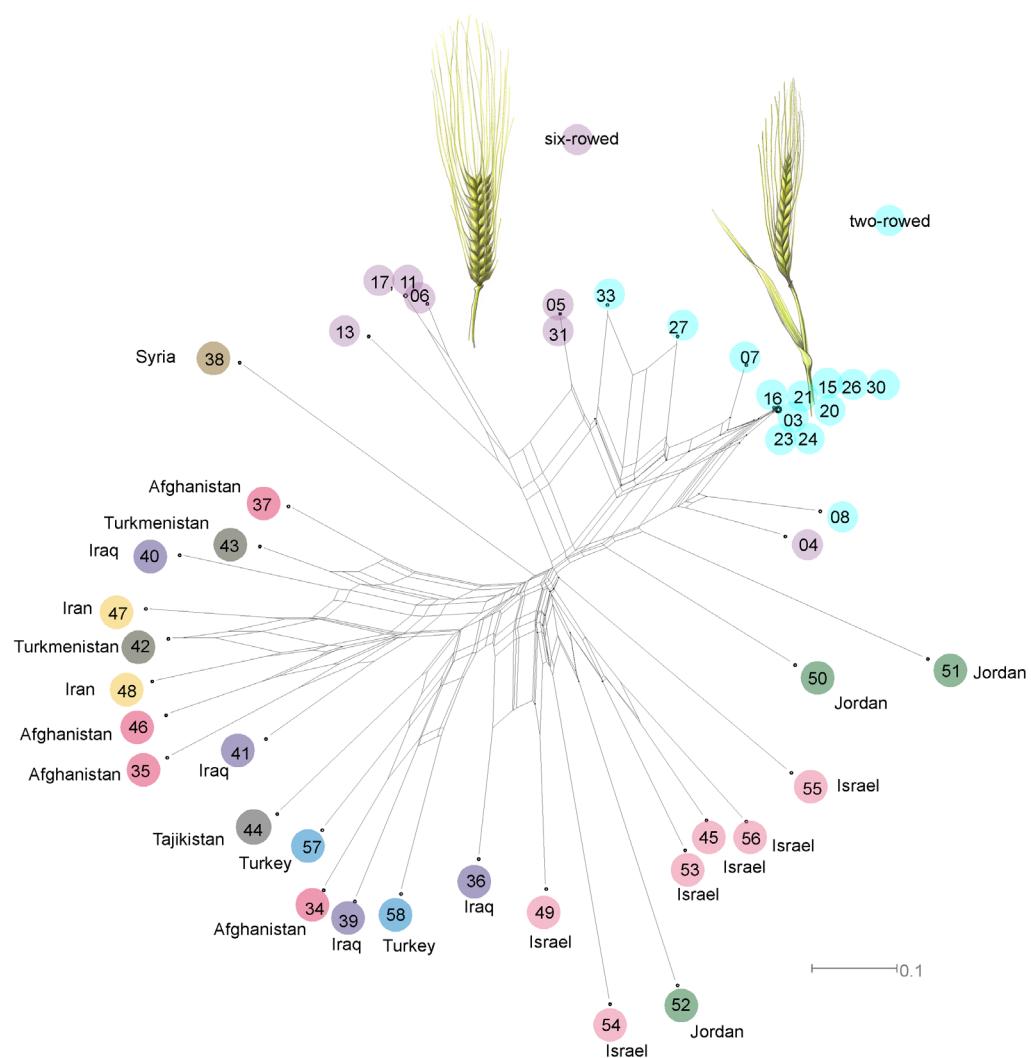
Loss of nucleotide diversity in domesticated barley

Gene fragments spanning a length from 663 to 945 nucleotides (table 2) were amplified in 25 W and 20 D lines for seven loci: *Adh2*, *Adh3*, *Amy1*, *Dhn9*, *GAPDH*, *PEPC* and *WAXY*. Sequence comparisons revealed that for the same gene multiple haplotypes existed with variable frequencies in W and D lines (table 4). All PCR amplification products were sequenced twice, no data were included if there were differences between the two. The occurrence of the same haplotype in several lines assigned a given sequence to a specific group, designated with a Roman numeral in table 4. The fewest number of haplotypes (five) was found at *PEPC*, the largest number (48) was found for *Adh3* (table 4).

The domesticated lines harbor fewer haplotypes. In total, 70 different haplotypes occur among the 25 wild lines, while only 17 occur among domesticated lines. Wild lines had, on average, ten haplotypes per locus (range 4–17) whereas the domesticated lines had 2.43 (range 1–4). Among the 17 D haplotypes found, six (35%) were not present in the 25 W line sample: *Adh2*-III, *Dhn9*-III, *GAPDH*-II, *GAPDH*-III, *WAXY*-II and *WAXY*-IV. These apparently D-specific haplotypes are very likely to be present in the W gene pool, should more individuals be tested. Their absence at *WAXY*, where 17 wild haplotypes were scored, indicate that the domesticated forms have sequestered a rare wild allele.

All loci sampled revealed a reduction of π and Θ_w in D–W comparisons, except *GAPDH* (table 5), the

Fig. 1 - Haplotype sequence relationships among wild *Hordeum spontaneum* and domesticated *H. vulgare* lines. **A** Neighbor-Net (NNet) planar graph of sequence similarity among 20 domesticated and 25 wild barley lines for the concatenated alignment of 5,616 sites. Line numbering corresponds to that in table 1. Geographical origins are indicated. Domesticated lines are boxed and labelled. Dotted circles designate WHC1, -2, and -3 (see text). The scale bar indicates sequence divergence. **B** Map showing geographical areas relevant to this study. Color coding of regions encompassing WHC1–3 and corresponding to sources of wild lines (Morrell et al. 2003) corresponds to that in (A). Barley ear drawings kindly prepared by S. Kilian.

A**B**

exception being due to the divergent haplotypes *GAPDH-II*, *GAPDH-III*, which are not present in the wild haplotype sample. For the remaining six loci, the loss of nucleotide diversity, $1 - \pi_d/\pi_w$ (Tenaillon et al. 2004) ranged from 69.2% at *WAXY* to 100% at *Dhn9* and *PEPC*, with an average of 87%. This is a substantially greater loss of nucleotide diversity than the value of 38% reported for maize domestication (Tenaillon et al. 2004). The loss of haplotype diversity, the corresponding reduction in number of different haplotypes, was 76% in the D–W comparison. Also the value of the d_{DW} statistics indicates a substantial loss of nucleotides diversity passing from wild to domesticated.

The lack of domesticated haplotype variants at *Amy1* and *PEPC* is notable, because both domesticated alleles are common (88 and 52% frequency, respectively) among the phenotypically wild (Salamini et al. 2002) lines sampled (table 4), hence they cannot be causally associated with the domesticated phenotype. A domestication sweep (human selection) at loci closely linked to *Amy1* and *PEPC* as the possible cause of lacking polymorphism at these loci cannot be strictly excluded but is also unlikely, given the small number of domestication loci known (Salamini et al. 2002) and the circumstance that 2/7 loci sampled had one D haplotype only. Taken together, these findings point to simple bottleneck effects at *Amy1* and *PEPC*, rather than selection. However, whether this bottleneck was incurred during the initial domestication process, or during subsequent barley breeding, cannot currently be determined. Reduction of diversity in the cultivated gene pool of barley has been previously reported by Bancock and Henry (2004), Molina-Cano et al. (2005), Russell et al. (2004), Tanno and Takeda (2004).

Evidence for selection?

Amy1 showed significant negative values of Tajima's D when all wild and domesticated sequences were considered (table 5), while *GAPDH* gave a significant positive value of Tajima's D in comparisons within domesticated lines (table 5). In principle, this could potentially indicate a deviation from neutrality, possibly due to positive (*Amy*) or balancing (*GAPDH*) selection. Indeed, there was an a priori expectation that we should be able to detect evidence for selection at *Amy1* because amylase activity is a key component of barley malt production, a trait that was enriched by human breeding. However, as Tajima (1989) has pointed out, the test is contingent upon the assumption that the population(s) in question has been in mutation-drift balance for a long evolutionary time, which is unlikely to apply in the current sample. Indeed, the wild accessions consist of individuals from diverse geographic ranges (not populations in the strict sense). Furthermore, Tajima (1989) has pointed out that if the taxa in question have experienced a bottleneck, Tajima's D can and will produce significantly positive or negative values (Tajima 1989; Wright and Gaut 2005) for genes that are selectively neutral. Hence the results of Tajima's test are also consistent with our hypothesis that bottlenecks due to domestication and breeding are the major determinants of polymorphism loss in the domesticated lines sampled.

If these sequences are in fact evolving neutrally in the wake of a bottleneck, how to account for the lack of nucleotide substitutions among *Amy1-I* and *PEPC-I* haplotypes? If we assume a grass nuclear substitution rate of 6.5×10^{-9} substitutions per site per year (Gaut et al. 1996) and furthermore assume that we have sampled fully 10,000 years per lineage in all *Amy1-I* and *PEPC-I* haplotype comparisons (Salamini et al. 2002), then we would expect to observe about one substitution per 7,500 sites. At *Amy1* and *PEPC* no substitutions were detected in about 15,000 freely mutable sites compared among domesticated lines (5,000 at *Amy1*, 2,560 in introns plus ~2,450 in coding regions; 10,000 at *PEPC*, 7,680 in introns and ~2,450 in

Fig. 2A - Neighbor-Net (NNet) planar graph of Hamming distances between binaric AFLP data from seven primer combinations, 295 polymorphic loci. The **B**. NNet planar graph of Hamming distances between haplotypes among wild *Hordeum spontaneum* and domesticated *H. vulgare* lines. Line designations are as in table 1 and fig. 1.

Table 4. Haplotypes and their frequencies (%) recorded at seven loci in 25 wild¹ and 20 domesticated lines

H	<i>Adh2</i>		<i>Adh3</i>		<i>Amy1</i>		<i>Dhn9</i>		<i>GAPDH</i>		<i>PEPC</i>		<i>WAXY</i>	
	W ²	D ²	W	D	W	D	W	D	W	D	W	D	W	D
I	28	10	4	60	88	100	20	0	15.4	60	52	100	11.1	65
II	4	70	4	15	4	0	8	65	0	10	4	0	0	15
III	0	20	4	25	4	0	0	35	0	30	4	0	3.7	10
IV	28	0	4	0	4	0	4	0	3.8	0	36	0	0	10
V	4	0	4	0	0	0	4	0	38.5	0	4	0	3.7	0
VI	4	0	4	0	0	0	4	0	3.8	0	0	0	3.7	0
VII	4	0	4	0	0	0	4	0	26.9	0	0	0	3.7	0
VIII	4	0	4	0	0	0	4	0	11.5	0	0	0	11.1	0
IX	4	0	28	0	0	0	32	0	0	0	0	0	3.7	0
X	4	0	4	0	0	0	8	0	0	0	0	0	3.7	0
XI	12	0	8	0	0	0	4	0	0	0	0	0	7.4	0
XII	4	0	8	0	0	0	4	0	0	0	0	0	3.7	0
XIII	0	0	8	0	0	0	4	0	0	0	0	0	7.4	0
XIV	0	0	4	0	0	0	0	0	0	0	0	0	3.7	0
XV	0	0	8	0	0	0	0	0	0	0	0	0	3.7	0
XVI	0	0	0	0	0	0	0	0	0	0	0	0	7.4	0
XVII	0	0	0	0	0	0	0	0	0	0	0	0	3.7	0
XVIII	0	0	0	0	0	0	0	0	0	0	0	0	3.7	0
XIX	0	0	0	0	0	0	0	0	0	0	0	0	14.8	0
H No	11	3	15	3	4	1	12	2	6	3	5	1	17	4

¹ Published sequence data for W lines were from Lin et al. (2001); Lin et al. (2002); Morrell et al. (2003).

² W wild lines D domesticated varieties

H No Number of haplotypes

coding regions). Thus, even if we had sampled the maximum amount of time possible with *Amy1*-I and *PEPC*-I haplotypes, we would only have anticipated two substitutions where none were observed. It is unlikely that all *Amy1*-I and *PEPC*-I haplotypes diverged 10,000 years ago, hence the lack of segregating sites is still consistent with domestication and breeding bottlenecks.

Revisiting the site of barley domestication

Badr et al. (2000) provided evidence from 400 AFLP loci using 317 wild and 57 domesticated *Hordeum* lines indicating that barley was, most probably, domesticated only once (see also Salamini et al. 2004), and that the Israeli–Jordan area is the region in which barley was brought into culture. This location is well outside the core area in southeastern Turkey (Lev-Yadun et al. 2000; Salamini et al. 2002), which is associated with several other plant domestication events of the Neolithic Near East area. Although the present data only encompass 25 wild (Lin et al. 2001; Morrell et al. 2003) and 20 domesticated lines, albeit at the level of sequences rather than AFLPs, we used it to readdress the site of barley domestication. Individually, the sequences of the seven genes sampled from 45 barley lines provided only a partial resolution, due to the small number of nucleotide differences both within wild accessions and between wild and domesticated lines (Supplementary fig. 1, Supplementary Material online).

Concatenating the available DNA sequences to an alignment of 5,616 bp per accession has the effect of mixing signals due to recombination or hybridization, which would be highly undesirable in tree-building approaches to sequence relationships. However, the NNet planar graph of sequence differences between

Table 5. Nucleotide diversity recorded at 7 Barley loci for 25 wild (W) and 20 domesticated (D) lines

Locus	All sites considered								Introns only (silent sites)					
	L	S		p ¹ x 10 ⁻³		d _{DW} ² x 10 ⁻³		Tajima's D ³	L	S		q _w x 10 ⁻³		
		W	D	W	D					W	D	W	D	
<i>Adh2</i>	836	17	2	3.98	0.93	3.56 (0.50)	-1.14	NS	388	4	1	2.73	0.73	
<i>Adh3</i>	809	45	1	20.88	0.62	19.24 (3.90)	+0.88	NS	321	21	1	17.33	0.88	
<i>Amy1</i>	661	9	0	1.52	0	0.79 (0.50)	-2.07 p<0.05		128	3	0	6.21	0	
<i>Dhn9</i>	724	14	1	3.59	0.66	2.90 (0.49)	-1.22	NS	473	11	1	6.16	0.60	
<i>GAPDH</i>	765	26	22	12.13	14.25	16.18 (1.88)	+2.60 p<0.05 ⁴		548	24	19	11.48	9.77	
<i>PEPC</i>	941	3	0	0.68	0	0.47 (0.11)	-0.83	NS	384	2	0	1.38	0	
<i>Waxy</i>	816	38	10	10.78	3.32	9.17 (1.19)	-0.95	NS	358	38	10	27.54	7.87	
Average				7.65	2.79							10.40	2.83	

L Number of sites, S number of polymorphic (segregating) sites, q_w Watterson's theta, NS not significant

¹ According to Nei (1987), equation 10.5.

² Average N° of nucleotide substitutions between D and W According to Nei (1987) using the Jukes and Cantor correction, standard deviation in parentheses.

³ Both W and D sequences considered, *Amy1* and *GAPDH* have a significant Tajima D test

⁴ Within D, the value is 2.84 (p<0.01); within W 1.28 (not significant).

individuals reveals three major groups of wild accessions sharing similar haplotype collections, which we designate as wild haplotype clusters (WHC-) 1, 2, and 3 in fig. 1A. It also uncovers the haplotype-sequence hybrid nature of the wild Tajikistan accession, which has a strong component of shared similarity both with WHC1 and with WHC3 (fig. 1A). WHC1 comprises wild lines from Israel, Jordan, and Syria. WCH2 contains wild lines reaching further East (Israel, Jordan, Turkey, and Iraq) and into the core area (indicated in fig. 1A). WHC3 contains lines collected from areas further East still, extending far beyond the primary habitat in the Fertile Crescent (indicated in fig. 1A), reaching into Turkmenistan (Morrell et al. 2003), but also includes an Israeli line, in agreement with the findings of Badr et al. (2000), who previously reported secondary migrations into Israel in their study of 374 barley lines.

The relationship of the domesticated Turkish lines to the wild lines is twofold: the two-rowed domesticated varieties (except line 8) share the haplotype collection of WHC1, whereas the six-rowed varieties (and the two-rowed line 8) share the haplotypes of WHC2. WHC3 is genetically distinct from the domesticated forms at these loci. Similar relationships are described by the maximum-likelihood tree (Supplementary fig. 1, Supplementary Material online). However, here the Tajikistan accession n° 44 (PI 293411) clusters within sequences belonging to WCH3: the tree shows only one signal, the NNet recovers two.

The WCH1, -2 and -3 clusters represent clusters of shared sequence similarity founded in discrete haplotype distributions and do not correspond to the West, Zagros, and East groups designated by Morrell et al. (2003) on the basis of geographical locations. The countries from which wild accessions were collected (see Morrell et al. (2003) for details) are shown in fig. 1B together with the ranges observed for members of WCH1–3. WHC1 and 2 both contain lines assigned to the West group, but as Morrell et al. (2003) point out, the main determinant of sequence similarity is not correlated to geographic distance.

With the exception of a single accession from Israel, probably reintroduced (Badr et al. 2000), WHC3 encompasses accessions that were collected outside the primary habitat in the Fertile Crescent and hence, like the wild Himalayan accessions (Badr et al. 2000), likely represent the result of human dispersal. There is no clear correlation between haplotype structure and geographical distance from the primary habitat in

WHC3, but it clearly represents a genotype distinct at these loci from those involved in domestication (fig. 1A).

In concatenated data, the structure of the network (or tree) is determined by distribution of the most divergent haplotypes among individuals, thereby severely skewing the result to reflect the nucleotide divergence signal represented by ancient but randomly assorted alleles. The same problem is encountered when allelic sequence variants at a single locus are analyzed with tree methods (Lin et al. 2001): sequence differences may take millions of years to accumulate but only one generation to reassort into new combinations. Standard measures typically applied to compare populations are inapplicable here, because the plants sampled do not constitute groups of preferentially interbreeding individuals (except perhaps the domesticated forms). In order to examine genotype relationships with deweighted effects from ancient alleles, we calculated the genetic distance between individuals as the proportion of different haplotypes per diploid genotype, thereby scoring haplotypes as either identical or different, regardless of the amount of nucleotide divergence between different haplotypes. This provided a much different picture of the relationships between wild and domesticated barley (fig. 2B), one in which two-rowed and six-rowed varieties again interleaved. But by scoring haplotypes as either identical or not, the domesticated forms clustered together, yet including two wild accessions from the Jordan valley (lines 50 and 51), in agreement with the independently obtained findings of Badr et al. (2000).

On the basis of haplotype diversity at seven loci in a sample of wild lines, the present data suggest that domesticated barley is genetically more similar to wild lines from the Jordan valley, which lies outside the core area in the Fertile Crescent. The domestication history of two-rowed and six-rowed varieties is unclear, but both types bear haplotypes that predominate in the Western Fertile Crescent. While our findings are in agreement with the previously inferred site of barley domestication in the Jordan valley (Badr et al. 2000), the new data open the possibility that barley domestication might have been diphyletic. Also AFLP data from the 20 D lines processed by the NNet procedure support the clear separation between two and six-rowed genotypes (fig. 2A). A diphyletic conclusion was previously excluded (Badr et al. 2000), but is favored by other authors (Molina-Cano et al. 2005 and citation therein) claiming independent barley origins for either two- versus six-rowed ears (Kolodinska Brantestam et al. 2004; Casas et al. 2005; Tanno and Takeda 2004), for brittleness of the rachis (Komatsuda et al. 2004), for hulled-naked caryopsis (Taketa et al. 2004), and for western or eastern cultivated barleys (Komatsuda et al. 2004). This particular matter concerning single versus multiple origins of barley is, however, complicated by the fact that (1) multiple independent introgression of genes from wild relatives to cultivated varieties can mimic multiple domestication events (Abdel-Ghani et al. 2004; Badr et al. 2000, Kanazin et al. 2002); (2) splitting of domesticated genotypes in two alternatives groups may have followed, and not be coeval with, the domestication process.

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Supplementary information

Manuscript information: Sequence data from this article have been deposited in GenBank Data library under accession nos. DQ195928 to DQ196067.

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Supplementary Material

I. Supplementary Tables

Supplementary Table S1. Pedigree, use and growth habit of 20 Turkish barley cultivars

Supplementary Table S2. Barley-primer used for amplification and sequencing

II. Supplementary Figure

Supplementary Figure S1 - Phylogenetic tree (maximum-likelihood) derived as described in the text.

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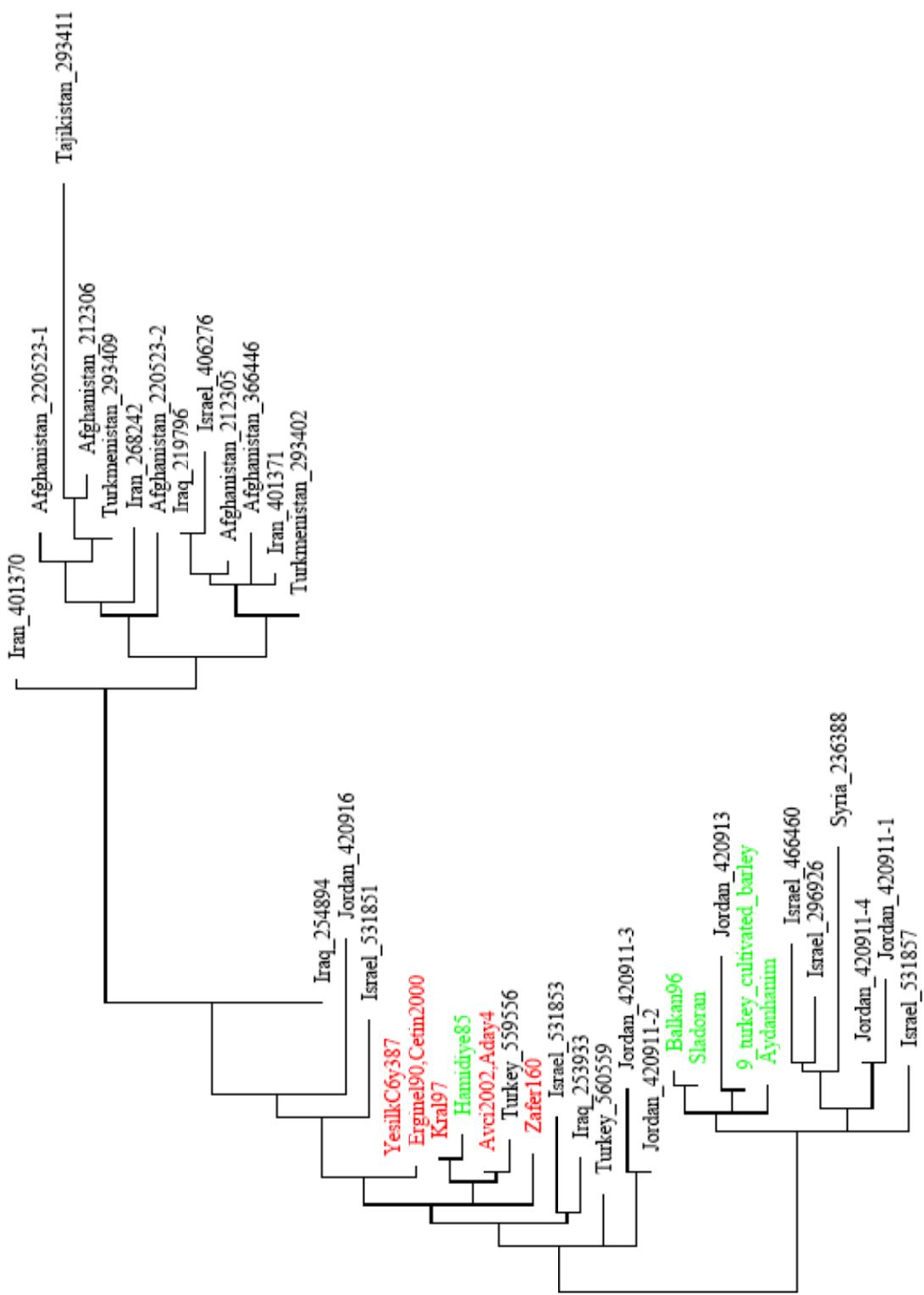
Supplementary table 1. Pedigree, use and growth habit of 20 Turkish barley cultivars

Domesticated varieties	Pedigree	Use	Growth habit
Tokak 157/37	Selection from Turkish land races	Feed	Winter
Kıral 97	Land race	Feed	Winter
Avcı 2002	Sci/3/Gi-72AB58,F1//WA1245141	Feed	Winter
Yesilköy 387	Zafer160 / land race from Kırklareli (gene bank no 3351)	Feed	Winter
Aydanhanım	GK Omega / Tarm 92	Malting	Winter
Hamidiye 85	Tokak mutant 173 TH / Tokak	Feed	Winter
Çetin 2000	Star (Iran) / 4875 no line	Feed	Winter
Zafer 160	Selection from Turkish land races	Feed	Winter
Çumra 2001	Tokak selection / Beka	Malting	Winter
Angora	(Triax / line 818 no) / (Malta X Ungar) /2/ (lineno 818 / Sultan)	Malting	Winter
Erginel 90	Escourgeon / Hop2171 (France)	Feed	Winter
Karatay 94	3896/I-3/Toplani/3/Rekal/1128/90 Manhaists	Feed/Malting	Winter
Tarm 92	Tokak / land races no 4875	Feed Malting	Winter
Yeşevi 93	Tokak / land race no 4857	Feed	Winter
Kalaycı 97	Erginel 9 / Tokak	Feed	Winter
Efes 1	Not described		
Sladoran	Introduction from Yugoslavia	Malting	Winter
Sahin 91	Unknown	Feed	Winter
Aday 4	Not described		
Balkan 96	Unknown	Malting	Winter

(Source: Cultivar Registration and Seed Certification Office archives, Ankara, Turkey)

Supplementary Table 2
Barley-primer used for amplification and sequencing

Primer-name	Primer-sequence
B104-1131FOR	CCT CGT TTC ACC AAA TAG CTT C
B106-1967REV	GTC CTT CGG GTT CAC AAA GTC
B201-109FOR	AAG GGC GCC TAG TTA ATC TAA TG
B202-933REV	ACA GCT AAG GAG GCA GAC TTT G
B306-86FOR	CAG TTC TCC ATC GTA CTC TTC G
B307-748REV	AGG TTG AGG TGG TCG ATG TC
B503-83FOR	AAT AGA ACG CCG AGC TAA TCT G
B504-834REV	TCC TTG ATC TTC TCC TTC ATG C
B604-199FOR	GCA TAC CTG CTT CTG TTG TTC C
B605-963REV	ACC TGA AGC AAC CAA ACA CAC
B704-1086REV	ATC ACC TCC TTG GAC AGA TGG
B705-132FOR	TCA ATA TGT TGC AAA CCT GGA C
B806-436FOR	CGG AGA TCC TGA AGG AGG AG
B807-1301REV	CTC CCA GTT CTT GGC AGG TC



Supplementary Figure 1. Phylogenetic tree (maximum-likelihood) derived as described in the text

Chapter 10

General summary, concluding remarks and future prospects

General Summary

Archaeological and genetic evidence indicate that western agriculture began in Fertile Crescent about 12,000 years ago (Zohary and Hopf 2000; Salamini et al. 2002). The widely accepted view today is that the process of crop domestication was slow, spanned up to one millennium and entailed multiple domestication events (Tanno and Willcox 2006). Local wild populations were domesticated in a core area and were then gradually dispersed throughout the region (Abbo et al. 2006). All current domestication models predicted a reduction of genetic diversity in domesticate forms compared to their wild progenitors (Doebley et al. 2006), but evidence to support that view from studies sampling large numbers of plants and loci were lacking. The keys obtaining deeper insights to plant domestication using molecular biology are I) comprehensive germplasm collections covering the whole distribution area for each species; II) comparing many wild and domesticated accessions per species; III) using molecular markers at many loci and modern high throughput techniques.

The present cumulative dissertation aimed to attain those goals. During this study, eight publications were submitted. Six papers are printed or published online.

Chapter 1. Evolutionary history of wheats - the main cereal of mankind

The main aim was to put together results of two independent wheat studies (Golovnina et al. (2007) and Kilian et al. (2007) using nuclear and chloroplast markers for all known wheat species. Based on this a slightly changed view on wheat evolution has been presented.

Chloroplast marker *matK* and *trnL* (tRNA - Leu) intron gave further support that *Aegilops speltoides* provided the cytoplasm for all polyploid wheats. Genome specific nuclear fragments at *ACC1* and *PGK1* loci have been used for all *Triticum* species. No variability was found at these two loci within polyploid wheats, however three haplotypes were detected in diploid wheats: I) one haplotype was shared between *T. urartu* and all polyploid wheats, this gave further support that *T. urartu* is indeed the donor of the wheat A genome; II) the second haplotype is close related to that of *Ae. speltoides*; III) the third one is unique for wild diploid wheats and supports that *T. boeoticum* is the wild progenitor of *T. monococcum*. This study further presents new evidence on long persisting haplotypes in diploid wheats.

Chapter 2. Quantification of genetic relationships among A genomes of wheats

The ultimate goal was to compare the A genomes of diploid wheats with that of tetraploid and hexaploid wheats and to quantify their genetic relationships by AFLP fingerprinting. Seven AFLP primer combinations produced 239 genome A specific bands for analysis. The results indicate that I) the *T. urartu* genome is more related to the A genomes of polyploid wheats than the genome of *T. boeoticum/ T. monococcum*; II) *T. dicoccum* and *T. durum* cluster together supporting a common origin; III) hexaploid hulled spelts cluster intermediate between tetraploid and hexaploid wheats; IV) AAGG wheats cluster distant from both diploid and other polyploid wheats and V) the *T. urartu* genome is about 20% closer 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*.

Chapter 3. Independent wheat B and G genome origins in outcrossing *Aegilops* progenitor haplotypes

The challenge was to determine if *Aegilops speltoides* was the donor of the B and G genomes in AABB and AAGG tetraploids. We studied molecular diversity in a large *Aegilops* collection using genome specific AFLP loci and haplotypes. The identification and use of B genome specific markers allowed us to pinpoint the origin of the wheat B genome to S chromosomes of *Ae. speltoides*. It is shown that 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 reveal that the B and G genomes of polyploid wheats are unique samples of *Ae. speltoides* haplotype diversity. These have been sequestered by the AABB *T. dicoccoides* and AAGG *T. araraticum* lineages during their independent origins.

Chapter 4. Geography and domestication of wild emmer wheat (*T. dicoccoides*)

This invited review to celebrate the 100th anniversary of the discovering of wild emmer wheat (*T. dicoccoides*) by Aaron Aaronsohn in nature summarizes the recent knowledge on geography and domestication of that important wild wheat that is critical for the bread wheat history. The most important contribution of that paper is the distribution map, combining all important published maps, but including also our own observations in nature. This map is color-coded and presents all wild emmer groups identified by Ozkan et al. (2005). Furthermore, the possible area where two wild emmer races are expected to overlap is visible. This map will provide useful help for further targeted collection trips on wild emmer wheat.

Chapter 5. Estimating genetic diversity in durum and bread wheat cultivars from Turkey using AFLP and SAMPL markers

In this pilot study on genetic diversity for cultivated wheats released in Turkey, 12 hard wheats (*T. durum*) and 22 bread wheats (*T. aestivum*), were investigated by five AFLP and three SAMPL primer combinations. The results indicate that the genetic diversity is very limited within the Turkish wheat cultivars. However, the durum wheat accession Kunduru-1149 and the bread wheat accession Ikizce-96 are distant from all other wheats and provide good potential to enrich the cultivated Turkish wheat gene pool for future breeding.

Chapter 6. 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

This study was the focus of the dissertation. The aim was to study nucleotide diversity using an extended germplasm collection, including also re-collected wild accessions from the Karacadag mountain range. We found unexpected results that will contribute to the ongoing discussion on domestication.

We sequenced 18 loci across 321 wild and 92 domesticate einkorn lines. This is the most comprehensive study published so far. Our data reveal that wild einkorn underwent natural genetic differentiation, prior

domestication and we identified three races of wild einkorn wheat. Two outstanding results were obtained, making einkorn wheat a superior model for crop domestication: I) we identified the natural progenitor (or at least the wild sister group) of domesticated einkorn wheat. Only the β race was exploited by humans for domestication; II) we found no evidence for a reduction of nucleotide diversity during domestication, because nucleotide diversity in domesticate einkorn is higher than in its wild sister-group β . This is in sharp contrast to all previous findings among more intensely bred crop species. Based upon combining our data with recent archaeological findings, we were also able to present a new model of einkorn domestication, indicating that a specific wild einkorn race was subjected to multiple independent domestication events which anticipates its spreading out of the Fertile Crescent.

Chapter 7. Natural variation and identification of microelements content in seeds of einkorn wheat (*Triticum monococcum*)

The task of this work was to study micronutrient variation in einkorn wheat in order to identify accessions suitable for subsequent breeding to provide crops with increased micronutrient contents.

We studied 54 einkorn wheat accessions for Zn, Fe, Mn and Cu contents. 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.

Chapter 8. Haplotype structure at seven barley genes: relevance to gene pool bottlenecks, phylogeny of ear type and site of barley domestication

The aim was to detect nucleotide diversity among 20 representative domesticated barley (*Hordeum vulgare*) accessions, including 13 two-rowed and 7 six-rowed varieties and to compare them with 25 wild accessions (*H. spontaneum*) at seven loci.

In comparisons of wild versus domesticated barley, the number of haplotypes, the average nucleotide diversity π , and Watterson's theta at silent sites were reduced in domesticated lines. These values provide evidence that nucleotide diversity is reduced in domesticated barley, probably due to continuous breeding since its domestication. Phylogenetic networks uncover distinct wild and domesticated barley groups and support the view that barley may have been domesticated in the Jordan valley, but provide also new data for independent domestications of two-rowed and six-rowed barley.

Concluding Remarks and Future Prospects

It is an exciting time for the study on natural variation and domestication of crop plants. New technologies and new genomic resources became available in the last few years and previously unasked questions are now being investigated. This has already contributed to our present understanding of plant domestication. Wild progenitors for several crops were identified and the regions of domestication are known. Einkorn remains unique at the moment, because a wild einkorn race that was domesticated by humans was identified within the whole wild einkorn gene pool. Furthermore, no reduction of nucleotide diversity during the domestication process was evident, speaking for multiple independent domestication events for the same einkorn race. Currently, screening large germplasm collections for emmer and barley is in progress. This in turn will provide hints as to whether the einkorn domestication model might be applicable to other crops.

However, several questions remain to be solved. Among the most important for cereal breeding is the issue of frequencies changed during domestication. On the other hand, new genomic resources for future plant breeding require that new agronomically important genes be isolated. International consortia, such as the International Triticeae Mapping Initiative (ITMI), the International Wheat Genome Sequencing Consortium (IWGSC) or the International Barley Sequencing Consortium (IBSC) will lead to accelerated gene discovery and will shed new light on mechanisms that have shaped the wheat and barley genomes during their evolution and domestication.

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Abstract

Archaeological and genetic evidences indicate that western agriculture began in Fertile Crescent about 12,000 years ago. The present dissertation has attained new insights and has contributed to ongoing discussions on plant domestication. During this study, eight publications were submitted. Six papers are printed or published online.

The first chapter describes a combined study on wheat evolution using nuclear and chloroplast markers for all known wheat species. Based on this a slightly changed view on wheat evolution is presented.

The work shown in chapter 2 quantifies the genetic relationship among A genomes of wheat. The data indicate that the *Triticum urartu* genome A is about 20% closer related to the A genomes of polyploidy wheats than the *T. boeoticum* genome.

Chapter 3 presents an important contribution on the search for the wheat genome B donor. The results provide strong evidence that the B and G genomes of polyploid wheats are unique samples of *Ae. speloides* haplotype diversity. These have been sequestered by the AABB *T. dicoccoides* and AAGG *T. araraticum* lineages during their independent origins.

The invited review shown in chapter 4 summarizes the recent knowledge on geography and domestication of wild emmer wheat (*T. dicoccoides*) and provides the most important distribution map for the species..

One pilot study on genetic diversity for cultivated wheats released in Turkey is presented in chapter 5. Two distinct accessions that provide good potential to enrich the cultivated wheat Turkish genepool for future breeding were identified.

The most important study is presented in chapter 6. The natural progenitor of domesticated einkorn wheat was identified, furthermore no evidence for a reduction of nucleotide diversity during domestication was found. This is in sharp contrast to all previous findings covering more intensely bred crop species. Based upon combining the data with recent archaeological findings, a new model of einkorn domestication is presented.

Chapter 7 describes a study on micronutrient variation in einkorn wheat. The results show large genotypic variation in micronutrient contents in seeds of einkorn.

The last study in (chapter 8) presents the haplotype structure at seven barley genes. In comparisons of wild versus domesticated barley, several values provide evidence that nucleotide diversity is reduced in domesticated barley, probably due to continuous breeding since its domestication. Phylogenetic networks uncover distinct wild and domesticated barley groups and support the view that barley may have been domesticated in the Jordan valley, but provide also new data for independent domestications of two-rowed and six-rowed barley.

Zusammenfassung

Archäologische und genetische Daten belegen, dass die Ursprünge unserer Landwirtschaft im Fruchtbaren Halbmond, vor circa 12,000 Jahren, zu suchen sind. Die vorliegende Promotionsarbeit hatte das Ziel, neue Einblicke in dieses Thema zu liefern. Während der Promotion wurden acht Publikationen eingereicht, sechs davon sind bereits gedruckt oder online publiziert wurden.

Das erste Kapitel beschreibt eine kombinierte Studie über die Evolution des Weizens. basierend auf Kern-, und Chloroplastengenom-Markern. Es konnten neue Einblicke in die Weizenevolution gewonnen werden.

Die im zweiten Kapitel vorgestellte Arbeit hatte das Ziel, die genetischen Beziehungen zwischen den Weizen A-Genomen zu quantifizieren. Die Daten zeigen, dass das A-Genom von *Triticum urartu* ungefähr 20 Prozent ähnlicher zu den A-Genomen der polyploiden Weizen ist, als das A-Genom von *T. boeoticum*.

Kapitel drei stellt einen wichtigen Beitrag in der Suche nach dem Weizen B-Genom-Donor vor. Die Ergebnisse zeigen, dass die B-, und G-Genome des polyploiden Weizens von *Aegilops speltoides* abstammen, die in unabhängigen Hybridisierungen mit *T. urartu* zu den tetraploiden Weizen führten.

Kapitel vier fasst das Wissen über die Geography und die Domestikation von wildem Emmer (*T. dicoccoides*) zusammen.

Eine erste Arbeit über die genetische Vielfalt von kultiviertem türkischen Weizen wird im Kapitel fünf aufgezeigt. Zwei Akzessionen konnten identifiziert werden, die gutes Potential besitzen um den türkischen Genpool anzureichern.

Die wichtigste Arbeit dieser Promotion wird im Kapitel sechs vorgestellt. Der natürliche Vorfahre des Einkornweizens konnte identifiziert werden. Weiterhin konnten keine Hinweise dafür gefunden werden, dass die Nukleotid-Vielfalt durch den Domestikationsprozess reduziert wurde. Ein neues Modell der Einkorn-Domestikation wird präsentiert.

Kapitel sieben zeigt eine Studie, in der Mikronährstoffe in Einkorn-Samen gemessen wurden. Die Ergebnisse belegen eine grosse Vielfalt an Mikronährstoffgehalten in Einkorn.

In Kapitel acht wird abschliessend eine Arbeit über die Haplotypenstrukturen in sieben Gerste-Genen vorgestellt. Es konnte gezeigt werden, dass die Nukleotid-Vielfalt in domestizierter Gerste niedriger ist als in wilder Gerste. Phylogenetische Netzwerke zeigen, dass Gerste möglicherweise im Jordangraben domestiziert wurde, sowie das zweizeilige und sechszeilige Gerste möglicherweise unabhängig voneinander domestiziert wurden.

Curriculum vitae

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Diploma (MSc)

10/2002: Institute of Botany, University of Jena, under the supervision of F. Hellwig and R. Oelmüller. Title: "Molekularbiologische Untersuchungen von Chloroplasten-genomen ausgewählter Vertreter der Monotropoideae".

<i>Undergraduate degree</i>	10/1995-10/2002: in Biology at the University of Jena major: Botany minors: Microbiology, Geology and Ecology
<i>Military service</i>	07/1993-06/1995: Mountain ranger in Berchtesgaden and Mittenwald. Since 1995, reserve status. Current rank: Captain (Reserve)
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(Picture: Hakan Özkan)

Die hier vorgelegte Dissertation habe ich eigenständig und ohne unerlaubte Hilfe angefertigt. Die Dissertation wurde in der vorgelegten oder in ähnlicher Form noch bei keiner anderen Institution eingereicht. Ich habe bisher keine erfolglosen Promotionsversuche unternommen.

Düsseldorf, den 27.10.2007

(Benjamin Kilian)