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Invited Review Article

Wild emmer wheat, *Triticum dicoccoides,* occupies a pivotal position in wheat domestication process

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Abstract

Domestication of plants and animals is the major factor underlying human civilization. Cultivated wheats refer mainly to two types: the hexaploid bread wheat (*Triticum aestivum*) accounting for about 95% of world wheat production, and the tetraploid durum wheat (*T. durum*) accounting for the other 5%. *T. aestivum* derived from a cross between domesticated emmer *T. dicoccum* and the goat grass *Aegilops tauschii,* which most probably originated in the south or west of the Caspian Sea about 9,000 years ago. *T. dicoccoides*, the wild emmer wheat, is the progenitor of cultivated wheats, has the same genome formula as durum wheat and has contributed two genomes to bread wheat, and has played a core role to wheat domestication. This process of wheat domestication fits the gradual and multi-site model rather than the fast and single-site model. Domestication has genetically not only transformed the brittle rachis, tenacious glume and non-free threshability, but also modified yield and yield components in wheat. Wheat domestication is only involved in a limited number of chromosome regions, or domestication syndrome factors, though many relevant quantitative trait loci were detected. The available crop genome sequences and genome sequencing of wheat can transform today's biology, dramatically advancing both theory and application of wheat domestication study. The nonrandom adaptive processes and complexes in *T. dicoccoides* and other wheat relatives could provide the basis for wheat improvement as single genes, QTLs, and interacting biochemical networks. Genome sequencing of diploid wild wheat, either *T. urartu* or *Ae. tauschii*, could be helpful for isolation of domestication syndrome factors and other relevant genes. The distinct adaptive complexes of *T. dicoccoides* to environmental stresses is of great importance for improvement of bread wheat.

Keywords: Cultivated wheat, Wild emmer wheat, Evolution and domestication, Major domestication gene, Domestication-related quantitative trait locus, Domestication syndrome factor, Gene-rich regions.

Introduction

Domestication of plants and animals dramatically promoted human cultural development and is the major factor underlying human civilization. Domestication performed by humans primarily during the last 10,000 years is a gigantic evolutionary experiment of adaptation and speciation generating incipient species (Darwin, 1905; Zohary and Hopf, 2000; Feldman and Kislev, 2007). It leads to adaptive syndromes fitting human ecology (Harlan, 1992). Domestication and the emergence of agricultural economies from pre-agricultural ones established human sedentism, urbanization, culture, and an unprecedented population explosion. Domestication makes all the cultivars, including wheat human-dependent, capable of surviving only under cultivation in human agricultural niches to meet human needs and culture. Wheat is the universal cereal of Old World agriculture and the world's foremost crop plant (Zohary and Hopf, 2000; Feldman et al., 1995; Gustafson et al., 2009), followed by rice and maize. Wheat was among the earliest domesticated crop plants, dating back 10,000 years ago in the pre-pottery Neolithic Near East Fertile Crescent (Harlan and Zohary, 1966). Modern wheat cultivars usually refer to two species: hexaploid bread wheat, *Triticum aestivum* (2*n* = 6x = 42, AABBDD), and tetraploid, hard or durum-type wheat, *T. turgidum durum* (2*n* = 4x = 28, AABB), used for macaroni and low-rising bread. Other species are relict (for a detailed account see Zohary and Hopf, 2000; Gill et al., 2006, 2007; Feldman and Kislev, 2007). Bread wheat accounts for about 95% of world wheat production. The other 5% is durum wheat. Today, wheat ranks first in the world's grain production and accounts for more than 20% of the total human food calories. Wheat is now extensively grown on 17% of all crop areas, in the temperate, Mediterranean-type, and subtropical parts of both world hemispheres from 67˚N to 45˚S. It is the major cereal crop of temperate regions and is the staple food for 40% of the world's population (faostat.fao.org; www.croptrust.org). The world's main wheat-producing regions are in temperate and southern Russia, the central plains of the US, southern Canada, the Mediterranean basin, north-central China, India, Argentina, and southwestern Australia. Human history is closely correlated with development of wheat, barley, and possibly rye because they belong to the Neolithic founder crops

from which western agriculture was built (Kilian et al., 2009). Wheat is also a superb model organism for the evolutionary theory of allopolyploid speciation, adaptation, and domestication in plants. Its domestication, primarily in modern breeding practices, led to its genetic erosion and increasing susceptibility and vulnerability to environmental stresses, pests, and diseases (Nevo, 2009; Fu and Somers, 2009). Hence, its future genetic improvement as a high-quality nutritional food is paramount for feeding the ever-increasing human population. The best strategy for wheat improvement is to utilize the adaptive genetic resources of the wild progenitors including wild emmer *T. dicoccoides* (Feldman and Sears, 1981; Nevo and Beiles, 1989). Due to high self-pollination, the genetic diversity of wheat is represented in the wild by numerous clones and in cultivation by some 25,000 different cultivars. Cultivated primitive forms have hulled grains, whereas advanced forms are free-threshing. Likewise, wild wheat has brittle rachis that make spikes disarticulate at maturity into individual spikelets. Each spikelet, with the wedge-shaped rachis internode at its base, constitutes an arrow-like device that inserts the seed into the ground (Zohary, 1969). By contrast, all cultivated wheat has non-brittle spikes that stay intact after maturation, depending on humans, for reaping, threshing, and sowing (Nevo et al., 2002). The free-threshing of cultivated wheat is regulated by the *Q* locus (Luo et al., 2000), located on chromosome 5A, and it may have arisen from the *q* gene of the hulled varieties by a series of mutations (Feldman et al., 1995). Wheat domestication occurred 10,000 years ago in the Fertile Crescent ushering in the beginning of agriculture and signifying an important breakthrough in the advancement of civilization. The economic importance of wheat has triggered intense cytogenetic and genetic studies in the past decades that resulted in a wealth of information and tools that have been used to develop wheat varieties with increased yield, improved quality, and enhanced biotic and abiotic stress tolerance. In contrast, genomics in wheat lagged behind other plant species, hampered by huge sizes (~17 Gb for the hexaploid wheat; ~12 Gb for the tetraploid wheat) and complexity (high repeat content, polyploidy) of the genomes. Recently, however, the situation has changed dramatically and the convergence of several technology developments led to the development of a ''Genomic toolbox'' with new and more efficient resources that supported the establishment of robust genomic programs in wheat. These new capabilities will provide a better understanding of wheat plant biology and support the improvement of agronomically important traits in this essential species (Feuillet and Muehlbauer, 2009; Paux and Sourdille, 2009).

Central role of wild emmer in wheat evolution

The family Poaceae (grasses) evolved 50-70 million years ago (Mya)(Kellogg, 2001; Huang et al., 2002) and the sub-family Pooideae including wheat, barley, and oats has diverged around 20 Mya (Inda et al., 2008). Wild diploid wheat (*T. urartu*, 2n = 2x = 14, genome AA) hybridized with goat grass (*Aegilops speltoides*, 2n = 2x = 14, genome BB) 300,000-500,000 BP (Huang et al., 2002; Dvorak and Akhunov, 2005) to produce wild emmer wheat (*T. dicoccoides*, 2n = 4x =28, genome AABB). The earliest evidence that man collected and used these cereals is from Ohalo II, a permanent site of epipaleolithic (19,000 BP) hunter-gatherers on the southwestern shore of the Sea of Galilee, Israel (Feldman and Kislev, 2007). Here, Kislev et al. (1992) found grains of wild barley and wild emmer, and Piperno (2004) presented evidence for grain processing and baking of flour. About 10,000 BP hunter-gatherers began to cultivate wild emmer. Subconscious plant selection slowly created a cultivated emmer (*T. dicoccum*, 2n = 4x =28, genome AABB) that spontaneously hybridized with another goat grass (*Ae. tauschii* (2n = 2x = 14, genome DD) around 9,000 BP to produce an early spelt (*T. spelta*, 2n = 6x = 42, genome AABBDD). About 8,500 BP, natural mutation changed the ears of both emmer and spelt to a more easily threshed type that later evolved into the free-threshing ears of durum wheat (*T. durum*, 2n = 4x =28, genome AABB) and bread wheat (*T. aestivum*, 2n = 6x = 42, genome AABBDD) (Fig. 1). It is accepted that *T. aestivum* originated from a cross between domesticated hulled tetraploid emmer *T. dicoccum* (or the free-threshing hard wheat *T. durum*, or the free-threshing *T. parvicoccum*) and the goat grass *A. tauschii* (DD) (Kihara, 1944; McFadden and Sears, 1946; Kerber, 1964; Kislev, 1980; Dvorak et al., 1998; Matsuoka and Nasuda, 2004). This cross should have taken place after emmer wheat cultivation spread east from the Fertile Crescent into the natural distribution area of *Ae. tauschii*. The cross occurred most probably south or west of the Caspian Sea about 9,000 years ago (Nesbitt and Samuel, 1996; Salamini et al., 2002; Giles and Brown, 2006). History of wheat evolution clearly shows that wild emmer wheat, *T. dicoccoides*, is located in the centre of the wheat domestication process.

Domestication of wild emmer wheat

Based on the ploidy level described above, wheat species can actually be divided into three groups: (i) diploid 2n = 2x = 14= einkorn wheat; (ii) tetraploid 2n = 4x = 28 = emmer wheat; and (iii) hexaploid 2n = 6x = 42 = common wheat or bread wheat (Sakamura, 1918; Sax and Sax, 1924; Kihara, 1924). There are two wild diploid *Triticum* species recognized as *T. boeoticum* (A^bA^b) and *T. urartu* (A^uA^u). The former is the ancestor of einkorn wheat *T. monococcum* but has been proved to be unrelated with cultivated tetraploid and hexaploid wheats (Gandilian, 1972; Johnson, 1975; Johnson and Dhaliwal, 1976; Dorofeev et al., 1979; Nesbitt and Samuel, 1996; Perrino et al., 1996; Heun et al., 1997; Dvorak et al., 1998a; Kilian et al., 2007; Ozkan et al., 2007). The latter, *T. urartu*, was never domesticated but played a critical role in wheat evolution and donated the A^u genome to all tetraploid and hexaploid wheats (Dvorak et al., 1993; Zohary and Hopf, 2000). The economically most important wheat is *T. aestivum* or bread wheat (A^uA^uBBDD). However, no wild hexaploid wheat has ever been found in nature, and only a semi-wild weedy form of hulled and brittle hexaploid wheat, *T. tibetanum*, has been discovered as a weed in barley and wheat fields (see Fig. 1; Kihara, 1944; McFadden and Sears, 1946; Kerber, 1964; Kislev, 1980; Shao et al., 1983; Nesbitt and Samuel, 1996; Dvorak et al., 1998a; Salamini et al., 2002; Matsuoka and Nasuda, 2004; Giles and Brown, 2006; Dubcovsky and Dvorak, 2007; Haudry et al., 2007; Fu and Somers, 2009). Wheat domestication occurred mainly in the wild tetraploid wheats (Fig. 1). There are two wild tetraploid wheat species known as *T. dicoccoides* and *T. araraticum*. They are similar in morphology, but different in their genomic constitution: *T. dicoccoides* has the genomic formula A^uA^uBB and *T. araraticum* A^uA^uGG (Zohary and Hopf, 2000). *T. dicoccoides*, wild emmer, naturally grows across the Fertile Crescent. Wild emmer wheat was rediscovered in nature by Aaron Aaronsohn (Aaronsohn and Schweinfurth, 1906). The first isolated spikelet of wild emmer was collected in 1855 by T. Kotschy but these spikelets were recognized as wild wheat only in 1873 by Kornicke who published his first note on it in 1889 (Kornicke, 1889). In 1906 Aahronson found an isolated specimen of wild emmer near Rosh Pinna, eastern Galilee (Aaronshon and Schweinfurt, 1906). The domesticated form of *T. dicoccoides* is known as *T.*

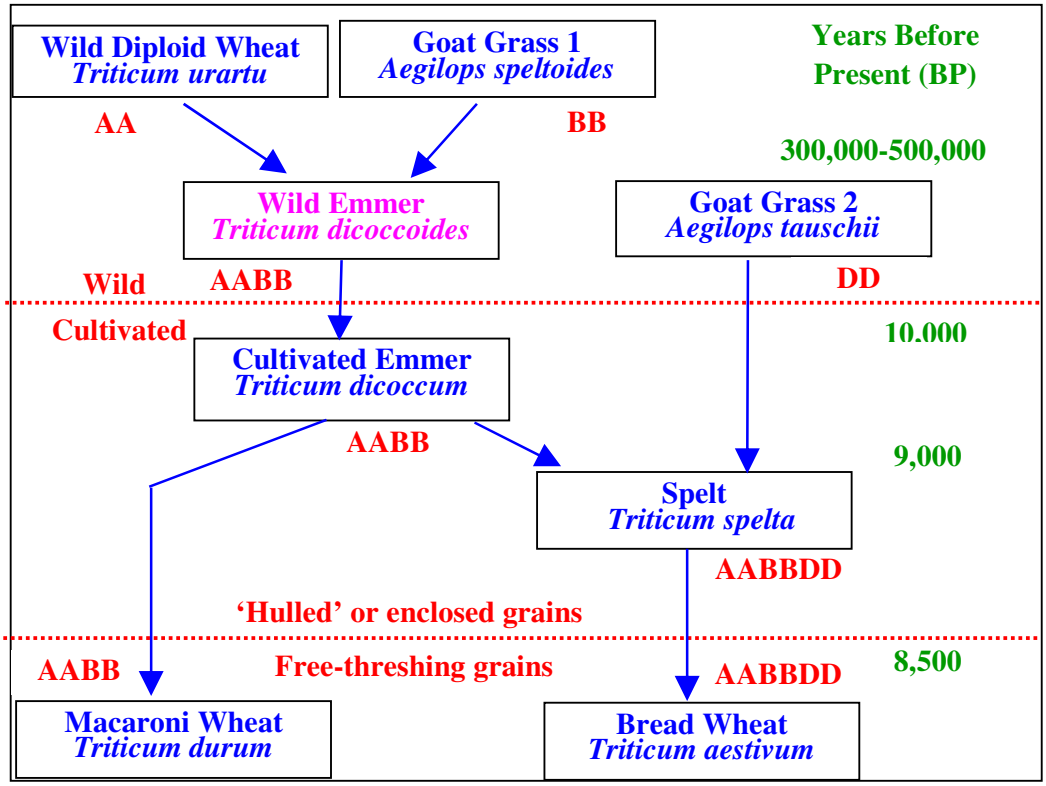

Fig 1. The diagram shows the evolution of wheat, from the prehistoric Stone Age grasses to modern macaroni wheat and bread wheat (adopted from http://www. newhallmill.org.uk/wht-evol.htm).

dicoccum (emmer, A^uA^uBB). The wheat was believed to be probably the domesticated in southeast Turkey (Ozkan et al., 2002, 2005; Mori et al., 2003; Luo et al., 2007). A reconsideration of the geography of domestication of tetraploid emmer wheats has been considered by Ozkan et al. (2005) and by Luo et al. (2007). Phylogenetic analysis indicates that two different races of *T. dicoccoides* exist: the western one, colonizing Israel, Syria, Lebanon and Jordan; and the central-eastern one, which has been frequently sampled in Turkey and rarely in Iraq and Iran. It is the central-eastern race that has played the role as progenitor of the domesticated germplasm (Ozkan et al., 2002; Mori et al., 2003; Luo et al., 2007), which indicates that the Turkish Karacadag population has a tree topology consistent with that of the progenitor of domesticated genotypes. However, we believe more in the multisite model of domestication of wild emmer and not in a single site in southeast Turkey. Nevo and Beiles (1989) studied *T. dicoccoides* and found no evidence for two races of *T. dicoccoides*. A review of archaeological findings from the Pre-Pottery Neolithic A (PPNA) (10,300-9,500 BP) indicates that wild emmer was first cultivated in the southern Levant (the western part of the Fertile Crescent). Domesticated emmer (with a non-brittle spike) appeared several hundred years later in the early PPNB (9,500-9,000 BP), and for a millennium or more was grown in a mixture with wild emmer in many Levantine sites. After the appearance of domesticated emmer, types with naked, free-threshing grains emerged in the late PPNB (9,000-7,500 BP). These archaeological findings of wild emmer cultivation and domestication do not support the idea of domestication within a small core area, but rather indicate the polycentric origin of agriculture in the Levant (Kislev et al., 1992; Feldman and Kislev, 2007). We strongly support the model of multiple-site independent domestication of wild emmer wheat across the Levant. According to this model, the genes for non-brittleness were transferred to numerous wild emmer genotypes through numerous spontaneous hybridizations, followed by human selection. Consequently, domesticated emmer wheat evolved as polymorphic populations rather than as single genotypes (Feldman and Kislev, 2007). Several cultivated tetraploid A^uA^uBB wheats were derived later from the domesticated emmer: *T. carthlicum* (Persian wheat), *T. polonicum* (Polish wheat), *T. ispahanicum*, *T. turanicum* (Khurasan wheat), and *T. turgidum* (English or pollard wheat). *T. dicoccum* was the favored crop for bread-making in ancient Egypt. Emmer wheat cultivation has significantly declined and can be found only in some traditional farming communities, mainly in Russia and Ethiopia. *T. durum* (macaroni or hard wheat) also originated from *T. dicoccum* somewhat later (Damania, 1998) and possibly independently (Salamini et al., 2002; Ozkan et al., 2005).

This free-threshing naked wheat is widely cultivated today for pasta production. The wild tetraploid wheats, including both *T. dicoccoides* and *T. araraticum* are distributed over the same area in the eastern part of the Fertile Crescent, Turkey, Iran and Iraq (Zohary and Hopf, 2000). These two species are morphologically indistinguishable (Tanaka and Ishi, 1973), and can be distinguished only by crossing or molecular tests. While *T. dicoccoides* crosses easily with cultivated tetraploid wheats, *T. araraticum* does not cross with *T. dicoccoides*, most probably due to relevant differences in the genome, like the existence of several translocations between B and G chromosomes (Feldman, 1966). *T. araraticum* was also domesticated but its cultivated form, *T. timopheevii* (A^uA^uGG; Timopheev's wheat), has been found in West Georgia together with the hexaploid wheat *T. zhukovskyi* ($A^mA^mA^uA^uGG$; Zhukovskyi's wheat). (Dorofeev et al., 1979). It is speculated

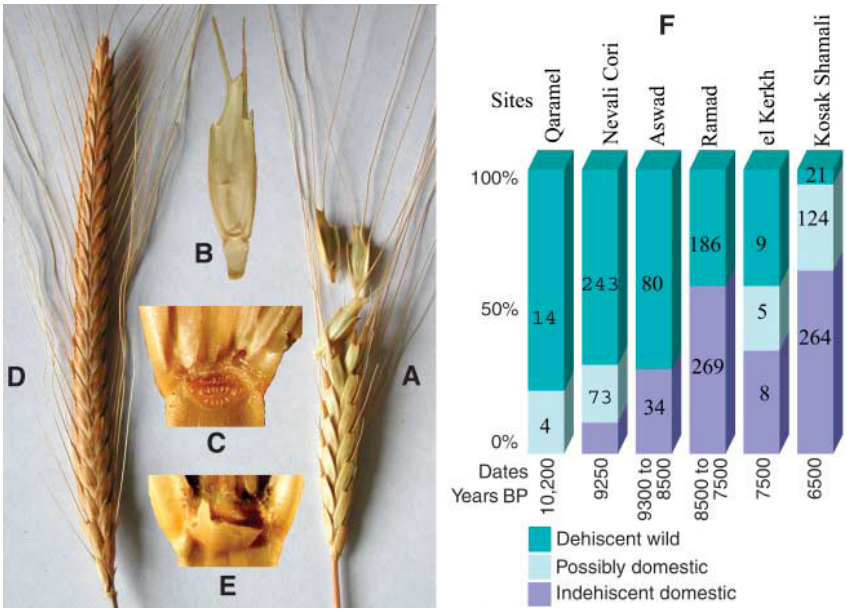

Fig 2. Modern examples of dehiscent wild einkorn wheat ear (A) and spikelet (B). Detail of spikelet with smooth wild abscission scar (C), indehiscent domestic ear (D), and detail of spikelet with jagged break (E) are shown. The bar chart (F) gives relative frequencies of sub-fossil finds with the absolute figures. Records from Aswad and Ramad (van Zeist and Bakker-Heeres, 1985) are of barley; the other four sites are of emmer wheat (adopted from Tanno and Willcox, 2006).

that when emmer cultivation spread to Transcaucasia, local populations of *T. araraticum* were colonizing as a weed in the fields of emmer crops and, by being incorporated into the agricultural cycle of harvest and sowing, became domesticated (Nesbitt and Samuel, 1996).

Most recently, Mori et al. (2009) found by using chloroplast SSR markers that *T. dicoccoides* is obviously more diverse that *T. araraticum*, and domesticated timopheevi wheat (*T. timopheevi*) had monophyletically originated from *T. araraticum*. The plastotypes revealed clear differences between the chloroplast DNA of timopheevi wheat and wild emmer wheat, and thus supported the hypothesis that these two wheat species originated independently. None of the *T. araraticum* plastotypes collected in Transcaucasia were closely related to the *T. timopheevi* plastotype. But the plastotypes found in northern Syria and southern Turkey showed closer relationships with *T. timopheevi*. Therefore, the domestication of timopheevi wheat might have occurred also in the Fertile Crescent region including southern Turkey and northern Syria other than in Transcaucasia (Mori et al., 2009).

Speed of emmer wheat domestication

The earliest cereal gathering or wheat domestication occurred in the Near East 19,000 years before the present (yr B.P.) (Kislev et al., 1992; Tanno and Willcox, 2006; Feldman and Kislev, 2007). Conventionally, wheat domestication studies have been focusing on a few quality traits (brittle rachis, tough glume, and free-threshing) controlled by single major genes (Br/br**,** Tg/tg, and Q/q, see Fig. 3). If ancient wheat breeders or farmers only selected the non-shattering or indehiscent, soft glume and free-threshing mutants in the wild wheat populations, the wheat plant would have been domesticated in a very short period, or the domestication should have been a rapid event. Hillman and Davies (1990) performed natural selection of barley, einkorn, and emmer wheat under primitive farming and concluded that perhaps only 20–30 years would be enough to completely domesticate these plants. Honne and Heun (2009) believe this conclusion is appropriate. The fact that the archaeobotanical record shows that remains of wild and domesticated forms of the same plant overlap for a long time (up to 3,000 years) appears inconsistent with rapid domestication (Tanno and Willcox, 2006; Balter, 2007; Willcox et al., 2008). The earliest indehiscent domestic wheat has been recognized in archaeological levels dated to ~9250 yr B.P. How long was wild emmer wheat cultivated before this date? Estimates vary from less than 200 (Hillman and Davies, 1990) to at least several hundred years (Kislev, 2002). A recent archaeological study conducted in northern Syria and southeastern Turkey indicated that indehiscence took over one millennium to become established events (Tanno and Willcox, 2006, Fig. 2). This means that early farmers did not only focus on indehiscence, but also on other important quantitative traits, e.g. spike size, heading date/growth duration, plant height, grain size, etc., in the harvest process of wild wheat. Measurements taken from ancient grains demonstrate that the size of wheat and barley grains remained essentially the same between 9500 and 6500 yr B.P. (Willcox, 2004). Therefore, selection for large cereal grains was slow because grain size was controlled by polygenes (Peng et al., 2003) and thus depended more on the position on the ear and the coupling of environmental conditions and genetic diversity than solely on genetic diversity. If early farmers harvested spikes after the ears began to shatter, indehiscent mutants would be rapidly adopted. But farmers probably harvested before the spikelets fell to avoid loss and paid close attention to important agronomic and economic traits (yield and yield components, plant height and heading date, etc.), thus indehiscence was not advantageous. Furthermore, when crops failed, farmers would have had to gather spikes from the wild. These two practices lowered the probability of the rare indehiscent mutant being selected. Domestication was a series of events occurring at different places over thousands of years, during which wild emmer wheat persisted in cultivated fields. Therefore, the

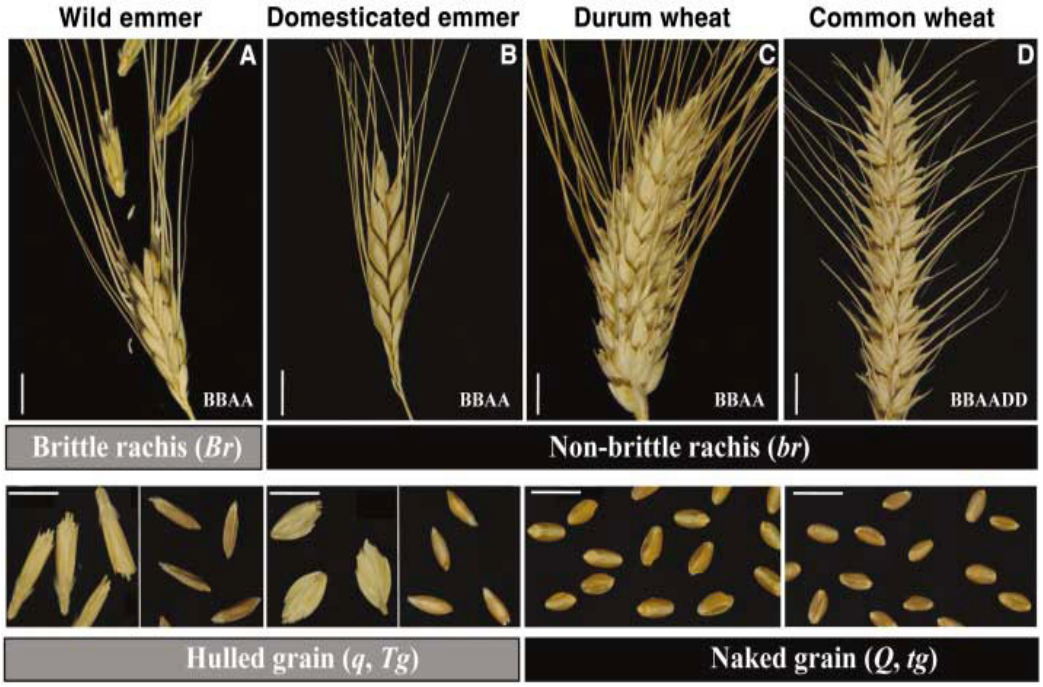

Fig 3. Wheat spikes showing (A) brittle rachis, (B to D) non-brittle rachis, (A and B) hulled grain, and (C and D) naked grain. (A) Wild emmer wheat (*T. dicoccoides*), (B) domesticated emmer (*T. dicoccum*), (C) durum (*T. durum*), and (D) common wheat (*T. aestivum*). White scale bars represent 1 cm. Letters at the lower right corner indicate the genome formula of each type of wheat. Gene symbols: *Br*, brittle rachis; *Tg*, tenacious glumes; and *Q*, square head. (adopted from Dubcovsky and Dvorak, 2007)

process of wheat domestication was slow, spanning over one thousand years, occurring in multiple sites of the Fertile Crescent, and fitting a gradualist and multi-site model (Fig. 2; Tanno and Willcox, 2006; Feldman and Kislev, 2007). This multi-place and long period of domestication seems much more realistic than the fast domestication. Furthermore, domesticated grasses, changes in grain size and shape evolved prior to non-shattering ears or panicles. Initial grain size increases may have evolved during the first centuries of cultivation, within perhaps 500–1,000 years. Non-shattering infructescence was much slower, becoming fixed about 1,000–2,000 years later (Fuller, 2007; Balter, 2007; Willcox et al., 2008).

Genetic and genomic dissection of major qualitative domestication traits

There are significant differences between domesticated cereal crops and their wild relatives. Many of these differences are apparently due to the intentional selections of humans. The most important wheat qualitative traits affected by domestication were the brittle rachis, tough glume, and free-threshing state (Fig. 3).

Brittle rachis

The breakage of rachis sheds seeds at maturity of any wild forms of wheat. This trait is agriculturally deleterious, and thus transformation of brittle rachis (Br) to non-Br is perhaps the first sign of domestication in wheat (Peng et al., 2003). Loss of seed shattering was a key event in the domestication of major cereals (Konishi et al., 2006). The modification of the brittle rachis trait has been critical for the origin of agriculture and sedentary societies. In nature, the spikelets of the wild ears fall apart at ripening through fragmentation of the rachis (by shattering or disarticulation). This mechanism is necessary for seed dispersal and self-planting. In a tough, non-brittle rachis the formation of fracture zones at the rachis is suppressed until mature spikes are harvested by man. It is thought that the spikes of non-brittle mutated plants were consciously selected by early farmers and that their frequency increased constantly in cultivated fields. But this process was slow and establishment of the non-brittle ancient cultivar took over one millennium (Tanno and Willcox, 2006; Balter, 2007; Willcox et al., 2008). The brittle rachis was dominant to the tough rachis, and was controlled by a single gene (Fig. 3). In the cross of semi-wild wheat with *T. aestivum spp. spelta*, three genes interact to control three types of rachis fragility, i.e., semi-wild wheat-type, spelta-type and the tough rachis of common wheat. Semi-wild wheat differs from common wheat in rachis fragility. This wheat also differs from other wheats with fragile rachis (*T. aestivum ssp. spelta*, *macha,* and *vavilovii*) in the pattern and degree of rachis disarticulation (Cao et al., 1997). The brittle rachis character is mapped to the homeologous group 3 chromosomes in wheats (Watanabe et al., 2002; Salamini et al., 2002; Watanabe 2005; Li and Gill, 2006). In einkorn, this trait is under the control of two genes that segregate 15 brittle to 1 tough rachis in the F_2 progeny of wild × domesticated crosses (Sharma and Waines, 1980). Cao et al. (1997) identified a single dominant gene, *Br1*, responsible for rachis fragility in a feral form of *T. aestivum* from Tibet. The gene was later localized on chromosome 3DS (Chen et al., 1998), as supported by studies of a cross of *T. dicoccoides* × *T. aestivum* (Rong et al., 2000). Other dominant genes are *Br2* and *Br3* on chromosomes 3A and 3B, respectively (Cao et al., 1997; Chen et al., 1998; Watanabe and Ikebata, 2000). The mature spike rachis of wild emmer (*T. dicoccoides*) disarticulates spontaneously between each spikelet leading to the dispersion of wedge-type diaspores. By contrast, the spike rachis of

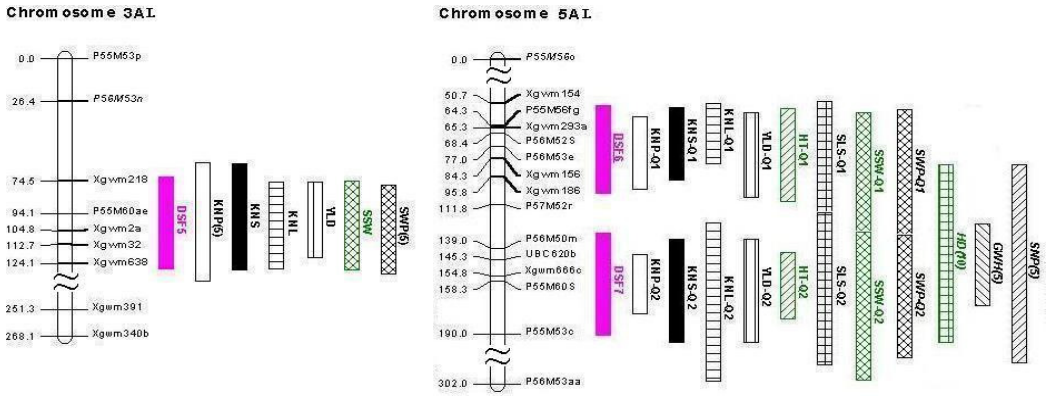

Fig 4. Map locations of DSFs and their involved QTLs in L version maps of wild emmer wheat, *T. dicoccoides*. Short arms of chromosomes are at the top. The domestication syndrome factors and the corresponding QTLs are shown on the right- hand side of the map: =domestication syndrome factor (DSF); = kernel number/spike, KNS; = kernel number/spikelet, KNL; = grain yield/plant, YLD; = plant height, HT; = spikelet number/spike, SLS; = single spike weight, SSW; = spike weight/plant, SWP; = kernel number/plant, KNP; = heading date, HD; = grain weight, GWH; = spike number/plant, SNP. The regular trait name represents a single QTL, the italic trait name represents a single QTL (Q2) detected by linked-QTL analysis, the regular trait name tailed with Q1 means the 1st QTL and tailed with Q2 means the 2nd QTL in a pair of linked QTLs. A (5) tailed a trait name means that the QTL effect is not significant at the level of 5% of FDR but is significant at the FDR=10%, whereas (10) means that the effect is not significant on the FDR=10%. (Adopted from Peng et al., 2003).

domesticated emmer (*T. dicoccum*) fails to disarticulate and remains intact until it is harvested. This major distinguishing feature between wild and domesticated emmer wheat is controlled by two major genes, *br2* and *br3,* on the short arms of chromosomes 3A and 3B, respectively (Nalam et al., 2006). The previously reported studies point to (i) multiple genetic pathways controlling the trait(s) and (ii) different genetic origins of loci controlling shattering in polyploids (Salamini et al., 2002). These considerations, combined with the mapping of QTLs for shattering, allow the analyses of microsyntenous relationships of these traits in the Triticeae and other grasses. Br in *T. dicoccoides* functions as an abscission layer in millet, seed dispersal in sorghum and maize, and seed shedding in rice (Peng et al., 2003).

Glume tenacity

Glume tenacity is another key trait closely related to the free-threshing habit and is modified by the domestication process in wheat. The wild emmer wheat floret is wrapped by tough glumes that make spikes difficult to thresh, whereas cultivated wheats have soft glumes and are free-threshing. Major and minor mutations were involved in the evolution of the free-threshing habit in hexaploid wheat (*T. aestivum*). The non-free-threshing habit of semi-wild wheat (*T. tibetanum*) was dominant to the free-threshing habit of common wheat, and glume tenacity of semi-wild wheat was controlled by a single gene in the cross of semi-wild wheat with the wheat cultivar Columbus. In the cross of semi-wild wheat with *T. aestivum spp. spelta*, the F_2 and F_3 population did not segregate for glume tenacity. Semi-wild wheat differs from common wheat in glume tenacity (Cao et al., 1997). The *Tg1* locus on chromosome 2D confers the free-threshing habit in hexaploid wheat (Kerber and Rowland, 1974). Genetic analysis showed that at least two genes controlled the free-threshing trait in crosses involving synthetic wheats (Villareal et al., 1996). Jantasuriyarat et al. (2004) detected several QTLs on chromosomes 2A, 2B, 2D, 5A, 6A, 6D, and 7B that significantly affect the free-threshing characteristic. However, the free-threshing habit was predominantly affected by a QTL on chromosome arm 2DS (corresponding to the *Tg1* gene) and, to a lesser extent, by a QTL on chromosome arm 5AL (corresponding to the *Q* factor). Recently, *Tg1* was mapped to a more precise location on the 2DS (Nalam et al., 2007). A recent study showed that the soft glume (*sog*) gene in a diploid wheat relative, *T. monococcum,* was found to be close to the centromere on the chromosome arm 2AS. But in common wheat the tenacious glume (*Tg*) gene of common wheat was located in the most distal region on the chromosome arm 2DS. The different positions suggest that the threshability mutations have independent evolutionary origins (Sood et al., 2009).

Free-threshing

The early wheat varieties were characterized by hulled seeds that required drying to be liberated from the chaff. When species characterized by a low degree of glume tenacity and by fragile rachis and free-threshing habit were selected by the farmers, harvesting grains became efficient. Free-threshing wheats have thinner glumes and paleas that allow an early release of naked kernels. After threshing, free grains are winnowed and stored ready for milling. Free-threshing varieties, like tetraploid hard wheat (*T. durum*), represent the final steps of wheat domestication. Major and minor mutations have been proposed to explain the evolution of the free-threshing habit in wheat (McKey, 1966; Jantasuriyarat et al., 2004). A major gene *Q* located on the chromosome arm 5AL inhibits speltoidy but also has pleiotropic effects on rachis fragility and glume tenacity. All non-free-threshing wild wheats carry the recessive *q* allele and all free-threshing tetraploid and hexaploid wheats

carry the dominant *Q* allele. In *T. aestivum*, the *Q* allele supports the formation of square-headed ears with good threshability, besides inducing softening of the glumes, reduction of ear length, more spikelets per ear, and toughness of the rachis (Sears, 1954; Snape et al., 1985; Kato et al., 1998, 2003). Disruption of the *Q* gene generates a *q* mutant phenotype, known as speltoid type because *q* mutants have tenacious glumes similar to that of spelt (*T. spelta; qq* genotype). Bread wheat lines harboring both *Q* and *q* alleles have intermediate phenotypes. Muramatsu (1963) also showed that the *q* allele is active by creating genotypes with 1–5 doses of either *Q* or *q* alleles. He showed that a square-headed hexaploid ear derives from either two doses of *Q* or five doses of *q*. In hexaploid wheat, the polygenic component controlling free-threshing is scattered throughout all three genomes. In tetraploid wheats, QTL studies identified four putative loci (Simonetti et al., 1999), located on chromosomes 2B, 5A, and 6A. Two of these QTLs correspond in position to the *Q* and *Tg* loci. A recent mapping effort led to the identification of two QTLs affecting both glume adherence and threshability (Nalam et al., 2006), suggesting that threshability is a function of glume adherence (Nalam et al., 2007). The abovementioned *Tg* controls the speltoid phenotype and inhibits the expression of *Q*. The suppression of the free-threshing character was thought to be due to a partially dominant *Tg* allele on chromosome 2D, derived from *Ae. Tauschii,* and thus leading to tenacious glumes. The conclusion is that free-threshing hexaploids have the genotype *tgtg*, *QQ* (Kerber and Rowland, 1974; Villareal et al., 1996; see Fig. 3).

Genetic and genomic analysis of quantitative domestication traits

Additional traits modified during domestication and the subsequent breeding process included quantitatively inherited traits such as grain yield, seed size, plant height, grain hardness, tillering capacity, seed dormancy, photoperiod, vernalization, and heading date. Furthermore, the spread of the domesticated emmer wheat from the Fertile Crescent required the adaptation to new environments supported by favorable alleles at critical genetic loci (Kilian et al., 2009).

Seed size

The evolution from small-seeded wild plants with natural seed dispersal to larger seeded non-shattering plants is evident. In domesticated grasses, changes in grain size and shape evolved prior to non-shattering ears or panicles. Initial grain size increases may have evolved during the first centuries of cultivation, within perhaps 500–1,000 years (Fuller, 2007). Seed size was strongly selected in all domesticated cereals: wheat, barley, oats, and rye in the Near East; maize in America; rice in Asia; and sorghum and millet in Africa (Peng et al., 2003). Seed size, and thus grain yield, was positively selected during domestication. The genetic control of seed size in domesticated versus wild tetraploid wheats was analyzed by using *T. dicoccoides* substitution lines in *T. durum* background (Elias et al., 1996). Kernel size is under a complex polygenic control, and genes with alleles contributing to increase and decrease in kernel size have been mapped to chromosomes 1A, 2A, 3A, 4A, 7A, 5B, and 7B. In an experiment with a cross of *T. dicoccoides* × *T. durum*, we mapped eight QTLs for grain weight/grain size on chromosomes 1B, 2A, 4A, 5A, 5B, 6B, 7A, and 7B. Major grain weight QTLs were located on chromosomes 2A, 4A, and 5B with LOD > 3.7 and $P \leq 0.001$. These three major seed-size QTLs correspond closely in sorghum, rice and maize, and another five QTLs correspond between two of these genera when the taxa are compared in a pairwise fashion. Parallel synteny existing between wheat and rice chromosomes indicates that all detected seed-size QTLs in *T. dicoccoides* correspond to their rice counterparts (Peng et al., 2003).

Developmental timing

Flowering time was also selected in the major cereals. Short-day flowering wild grasses were transformed into domesticates in which flowering time was unaffected by day length (Buckler et al., 2001). Heading date (HD)/flowering time is an important criterion for regional adaptation and yield in all cereals. The control of HD is critical for reproductive success and has a major impact on grain yield in Triticeae. Wild progenitors of domesticated cereals are well adapted to the prevailing environmental conditions in the Fertile Crescent. The first cereals domesticated in this region presumably showed the photoperiodic and vernalization phenotypes of their progenitors. However, during the domestication process and the spread of agriculture from the Fertile Crescent, novel adaptive traits suited for the new environments were selected. One key event was the selection of spring types that can be sown after winter. These spring types lack the vernalization requirement and show different responses to long days. Reduced photoperiod response is important in Europe and North America, where growing seasons are long (Turner et al., 2005). In our study, the wild parent, *T. dicoccoides*, was sensitive to day length and flowering was later than in the cultivar Langdon. Four HD QTLs were mapped on chromosomes 2A, 4B, 5A, and 6B (Peng et al., 2003). The wild allele for the QTL on 5A will increase the value of HD and so is responsible for the late flowering of *T. dicoccoides*, whereas the wild HD alleles on chromosomes 2A, 4B, and 6B can accelerate the flowering date. These "earliness" alleles, plus the early genes from the *T. durum* cultivar, might explain the significant transgressive segregation (the majority of the individuals were earlier than the early parent Langdon) for HD in the mapping population (Peng et al., 2003). In the long period of observation, we found that there is immense genetic variation in flowering time in *T. dicoccoides*. Wild emmer from Mt. Hermon in north Israel, e.g., accession H52, flower late in April and ripen in May whereas those from Gitit in the Samaria steppes in central Israel flower in February-March and ripen in April. Thus there is a widespread range in flowering in *T. dicoccoides* from cold (late) to warm (early) localities. In temperate cereals, *Vrn* and *Ppd* have been involved in domestication and adaptation to local environments. The evolution of spring types from a predominantly winter ancestral state is a key event in the post-domestication spread of temperate cereals (Cockram et al., 2009). On the basis of the map positions, it can be postulated that HD QTL on 5A may be similar to the *VRN1* gene mapped on chromosome 5A in *T. momococcum*. This gene is similar to the *Arabidopsis* MADS-box transcription factor *Apetala 1* (*AP1*), which initiates the transition from the vegetative to the reproductive state of the apical meristem (Yan et al., 2003). The HD QTL is located in a collinear position with the photoperiod response (*Ppd*) genes on the short arm of the group 2 chromosomes in wheat and barley. In common wheat, the allelic series of *Ppd* loci has decreasing potency from *Ppd-D1* to *Ppd-B1* to *Ppd* to *A1* (Worland, 1996). Further major photoperiod related genes/gene families appear to be conserved between barley and *Arabidopsis*, involving the GIGANTEA (GI), CONSTANS (CO), and FLOWERING LOCUS T (FT) genes in *Arabidopsis* and their orthologs in barley HvGI, HvCO, and HvFT (Griffiths et al., 2003; Dunford et al., 2005; Cockram et al., 2007; Faure et al., 2007). Nevertheless, none of

the grass QTLs associated with flowering time co-segregate with orthologous *Arabidopsis* "flowering" genes, i.e., different major determinants of photoperiod have been selected in the Triticeae (Börner et al., 1998; Griffiths et al., 2003).

Grain yield

Primary domestication targets were likely the genes that facilitated harvesting and enabled colonization of new environments. Yield must have soon assumed priority, minimizing labor input and land needs. Generally, the wild wheat *T. dicoccoides* has poor yielding potential. In a mapping population derived from *T. dicoccoides* × *T. durum*, the wild parent had a very poor yield of 0.5 g/plant that characterizes marginal, steppic populations of *dicoccoides*, whereas the domesticated parent had a much higher yield of 8.2 g/plant. Using an advanced QTL mapping software, *MultiQTL* (http://www.multiqtl.com), eight yield QTLs were mapped on chromosomes 1B, 2A, 3A, 5A, and 5B. Linked QTLs were detected on chromosomes 1B, 2A, and 5A, and they are highly significant (LOD = 5.5–10.1, $P \leq 0.001$). The eight yield QTLs overlapped with QTLs for other traits on chromosomes 1B, 2A, 3A, and 5A (Peng et al., 2003; Fig. 4). QTLs conferring *T. aestivum* yield traits were also mapped to chromosomes 3A, 4A, and 5A (Shah et al., 1999; Campbell et al., 2003; Araki et al., 1999; Kato et al., 2000). In a recent association mapping analysis, using simple sequence repeat (SSR) markers and a collection of bread wheat cultivars, QTLs for kernel size were detected on chromosomes 2D and 5A/5B (Breseghello and Sorrells, 2006).

Other quantitative traits modified through domestication

During the domestication process involving the above-described qualitative and quantitative traits, many other quantitative traits were also subjected to selections of ancient farmers via hitch-hiking effects. These traits include plant height (HT), spike number/plant (SNP), spike weight/plant (SWP), single spike weight (SSW), kernel number/plant (KNP); kernel number/spike (KNS); kernel number/spikelet (KNL); and spikelet number/spike (SLS). Using molecular markers and an advanced QTL mapping software, *MultiQTL*, we detected over 50 QTL effects for these eight traits in a wild emmer×durum wheat population (Peng et al., 2003).

Plant height is an extremely important target trait in modern wheat breeding since the "green revolution" in cereals was achieved by reducing plant height, thus the lodging susceptibility and increase in grain yield (Hedden, 2003). Modern wheats are short because they respond abnormally to gibberellin. The *Rht-1* gene in wheat encodes a repressor of GA signalling orthologous to *Arabidopsis GAI* (gibberellic acid "insensitive"), maize dwarf8 (*d8*), and barley Slender1 (*Sln1*) (Peng et al., 1999; Chandler et al., 2002; Hedden, 2003; Eastmond and Jones, 2005). Pleiotropic effects are not surprising for genes controlling hormone action and may be a common occurrence for the traits targeted by domestication and breeding (Cai and Morishima, 2002; Salamini et al., 2002). *Rht-B1b* and *Rht-D1b* genes on wheat chromosomes 4B and 4D are semi-dominant mutant alleles of the *Rht-1* gene conferring dwarfism (Hedden, 2003).

In addition, genes were identified that reduce plant height without affecting early growth, or coleoptile length and vigor. These genes were mapped to different wheat chromosomes, thus widening their exploitation in plant breeding (Ellis et al., 2005). However, dwarf wheat cultivars were used only in commercial production after the 1960s, and most of the wheat local races are tall. Therefore, ancient farmers did not select the dwarf but rather selected the tall mutants that had higher biomass and yielding potential during the domestication. Two pairs of linked QTLs for plant height were detected in chromosomes 5A and 7B, respectively, in our study. One of *T. dicoccoides* alleles on chromosome 5A could reduce plant height by 9.6-15.2 cm (Peng et al., 2003). Spike number is one of the most important yield components and greatly correlates with the tillering capacity in wheat. It must have undergone selection during the domestication. The grassy wild wheat, e.g., *T. dicoccoides*, usually has strong tillering ability and can be used as a source to increase the tillering capacity or spike number of wheat cultivars. In the *T. dicoccoides* × *T. durum* cross, seven QTL effects for spike number were detected in five chromosomes 1B, 2A, 2B, 5A and 7A, among which, 1B and 7A were the most significant and each carried a pair of linked QTLs, respectively (Peng et al., 2003). The genetic variation for tillering capacity was assessed for the wheat gene pool: low tillering genotypes frequently have a uniculm phenotype, enlarged spike, and modified leaf morphology (Atsmon and Jacobs, 1977). In wheat, a single recessive gene (*tin*) located on chromosome 1AS was found to control tiller number (Spielmeyer and Richards, 2004). This gene is perhaps a homoeologous allele of the striking spike number QTL on chromosome 1B of *T. dicoccoides* (Peng et al., 2003). Comparative genomics analyses revealed that *tin*, rice-reduced tillering mutations, and the barley *uniculm2* mutant map to nonsyntenic chromosomes (Rossini et al., 2006). Recently, a tiller inhibition gene *tin3* was identified and mapped to the long arm of *T. monococcum* chromosome $3A^m$ that is syntenic to a 324-kb region of rice chromosome arm 1L (Kuraparthy et al., 2007, 2008). Spike weight/plant (SWP) and single spike weight (SSW) are significantly correlated with each other, and also with grain weight/size and yield (Peng et al., 2003). Therefore, they were also subjected to selection during domestication. In the *T. dicoccoides* × *T. durum* cross, ten QTL effects were detected for SWP in six chromosomes with linked QTLs in chromosomes 1B, 2A, 5A and 7A, and five QTL effects were detected for SSW in four chromosomes with linked QTLs in chromosome 5A. Among these chromosomes, 5A and 2A for both SWP and SSW, and 1B for SWP are extremely important (Peng et al., 2003). Thus, highly significant domestication selection was applied to these chromosomes or chromosome regions. Kernel number/plant (KNP), kernel number/spike (KNS), kernel number/spikelet (KNL), and spikelet number/spike (SLS) are highly correlated with each other and also with yield (Peng et al., 2003). They are important yield components, thus should have been also subjected to selection during the domestication process. In our domestication QTL mapping effort, nine QTL effects for KNP were detected in six chromosomes with linked QTLs in 1B, 2A, and 5A; seven QTL effects for KNS were identified in five chromosomes with linked QTLs in 2A and 5A; seven QTL effects for KNL were found in six chromosomes with linked QTLs in 5A; and six QTL effects for SLS were detected in four chromosomes with linked QTLs in 5A and 6B (Peng et al., 2003). Among the relevant chromosomes, 5A is extremely important for all these four traits (LOD>6.0, P<0.0005), 2A is significantly important for KNP, KNS, and SLS (LOD>5.5, P<0.0005), and 1B is highly important for KNP (LOD>6.0, P<0.0005). Therefore, chromosomes 5A and 2A played a key role in domestication modification of these four spike-related traits. Interestingly, the above-discussed free-threshing gene *Q* is located in chromosome 5A (Luo et al., 2000). It is thus highly possible that the key domestication gene, *Q*, has pleiotropic effects on KNP, KNS, KNL, and SLS.

Domestication syndrome factors involving quantitative traits

Domesticated species differ from their wild ancestors and relatives for a set of traits, which is known as the domestication syndrome. The most important syndrome traits include growth habit, flowering time, seed dispersal, and gigantism (Frary and Doğanlar, 2003). In an effort to map quantitatively inherited domestication traits in emmer wheat, we found that most of the significant QTL effects are clustered mainly in a limited number of intervals in chromosomes 1B, 2A, 3A, and 5A. Consequently, the total number of intervals carrying domestication QTLs was only 16 though as many as 70 QTL effects were detected. The chromosomal regions harboring a cluster of domestication QTL are referred to as domestication syndrome factors (DSFs). Only seven DSFs, each involving a pleiotropic QTL or cluster of QTLs affecting 5–11 traits, were found in four chromosomes in wild emmer wheat (Fig. 4; Peng et al., 2003). Although most domestication traits are quantitatively inherited, the dramatic morphological changes that accompanied domestication may be due to relatively few genes (Frary and Doğanlar, 2003). A general transition from small-seeded plants with natural seed dispersal to larger-seeded non-shattering plants until harvest applies to all seed crops. Domestication genes have been functionally conserved over thousands of years and have similar, though not identical, effects in various species. These parallels transcend the deepest divisions within the angiosperms, with both monocot and dicot crops developing a similar adaptive domestication syndrome to human cultivation over the last 10,000 years (Harlan, 1992). The seven DSFs, in four of 14 chromosomes in tetraploid wheat, contained 80.4% of the 56 strong-to-moderate QTL effects underlying the differences between wild *T. dicoccoides* and cultivated *T. durum* for 11 traits (Peng et al., 2003). Independent domestication of sorghum, rice, and maize involved convergent selection for large seeds, non-shattering spikes, and day-length insensitive flowering. These similar phenotypes are largely determined by a small number of QTLs that closely resemble each other in the three taxa (Paterson et al., 1995). Thus, the limited number of DSFs of wheat (Fig. 4) corroborates the results in other cereal crops showing that the domestication syndrome is under relatively simple and rapidly evolving genetic control (Paterson et al., 1995).

Domestication syndrome factors and gene-rich regions

Gene distribution in *Triticeae* chromosomes is highly *nonrandom*, with a few gene-rich regions alternating with gene-poor regions, as in other eukaryotes. Gene-rich regions correspond to hot spots of recombination (Gill et al., 1996; a, 1996b Kunzel et al., 2000; Peng et al., 2004). The map positions of all seven wheat DSFs appeared to overlap with gene-rich regions (Fig. 5), and the key domestication gene, *Q*. Therefore, the high pleiotropy and/or tight linkage of most wheat domestication QTLs suggest an important role of recombination in either consolidation of positive mutations within the DSF clusters (Otto and Barton, 1997) or in reducing the antagonism between artificial and background (purifying) selection (Rice, 2002). The presumed coincidence between DSFs and gene-rich regions could facilitate component dissection of these factors, their further fine mapping, and finally map-based cloning.

Role of A and B genomes in wheat domestication

Inter-parental *Pst*I-based amplified fragment length polymorphisms (AFLP) showed that molecular markers are *nonrandomly* distributed among A and B genomes of tetraploid wheat: 60% of polymorphic AFLP loci were mapped to the B genome (Peng et al., 2000). Likewise, higher polymorphism in the B than in the A genome applies to microsatellites (Röder et al., 1998) and restriction fragment length polymorphism markers (Liu and Tsunewaki, 1991) in common hexaploid wheat as well as in *T. dicoccoides* in Israel (Li et al., 2000). However, in our wild wheat domestication QTL mapping study, both the number of QTL effects and domestication syndrome factors in the A genome significantly exceeded that in the B genome (Peng et al., 2003). The key domestication genes, *sos* and *Q*, are also located in A chromosomes (Luo et al., 2000; Sood et al., 2009). Therefore, wheat A genome has played a much more important role than the B genome in the wheat domestication process. These *nonrandom* distribution patterns of domestication-related genes/loci and DNA molecular markers may mirror the genetic differentiation of structure and function among genomes and chromosomes between *T. dicoccoides* and *T. durum* during domestication.

***Q* gene and its function**

Q gene is a major domestication gene conferring spike shape and threshability in wheat (Sears, 1954; McKey, 1966; Snape et al., 1985; Kato et al., 1998, 2003; Luo et al., 2000). This gene is also responsible for multiple quantitative spike traits such as spike weight, kernel number/plant, kernel number/spike, kernel number/ spikelet, and yield (Peng et al., 2003). Faris et al. (2005) and Gill et al. (2007) cloned the *Q* gene unraveling the structural and functional nature of the free-threshing trait and other early domestication events. The *Q* gene was shown to have sequence similarity to the *Arabidopsis* APETALA2 gene, thus a member of the AP2 family of plant-specific transcriptional regulators (Faris and Gill, 2002; Faris et al., 2003, 2005; Gill et al., 2007). This gene family regulates a diverse set of developmental traits in plants, but especially traits related to inflorescence structure and flowering. The cultivated (*Q*) allele is expressed at a higher level than the wild (*q*) allele, and gene dosage analysis indicates that differences in expression could be sufficient to explain the difference in phenotype. However, these alleles also differ by a single amino acid change that affects protein dimerization, suggesting that both regulator and protein function changes could be involved (Doebley et al., 2006). Further studies confirmed the association (Simons et al., 2006) and demonstrated that ectopic expression of *Q* in transgenic plants mimicked dosage and pleiotropic effects of *Q*. Increased transcription of *Q* was associated with spike compactness and reduced plant height. Previous research suggested that *Q* might have arisen from a duplication of *q* (Kuckuck, 1959). However, Simons et al. (2006) repudiate this hypothesis and showed that most probably *Q* arose through a gain-of-function mutation.

Importance of *Triticum dicoccoides* in wheat domestication and breeding

Wheat domestication increased food production, expanded sedentism and human population, and promoted development of early human civilization. Wheat cultivars are superior to most other cereals in their nutritive value. They contain 60-80% starch and 8-15% protein, which rise in elite wild genotypes of *T. dicoccoides* up to 13.9%-28.9% (Avivi, 1978, 1979; Avivi et al., 1983; Grama et al., 1983; Nevo et al., 1986; Levy, 1987). Wild emmer wheat is also extremely rich in high molecular weight glutenins (Nevo and Payne, 1987), thus an important source of elite baking quality. Wheat is the staple food for billions of people, and wild emmer wheat has unique bread-baking qualities. In the rapidly exploding world population (approaching 10 billion in 2050), wheat will continue to serve as the major food ingredient through bread

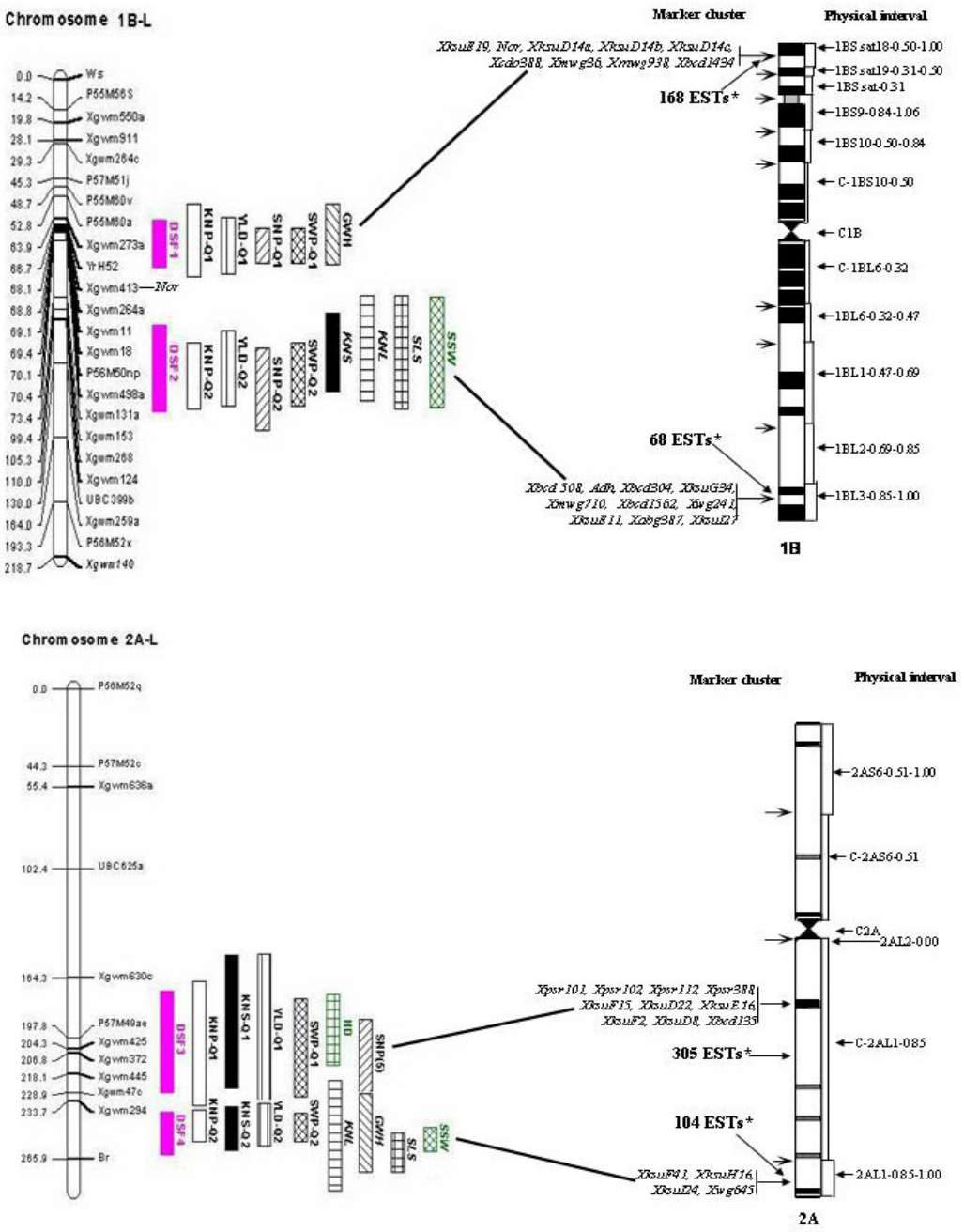

Fig 5. Location association between domestication syndrome factors and gene-rich regions in chromosomes 1B, 2A, 3A, and 5A.

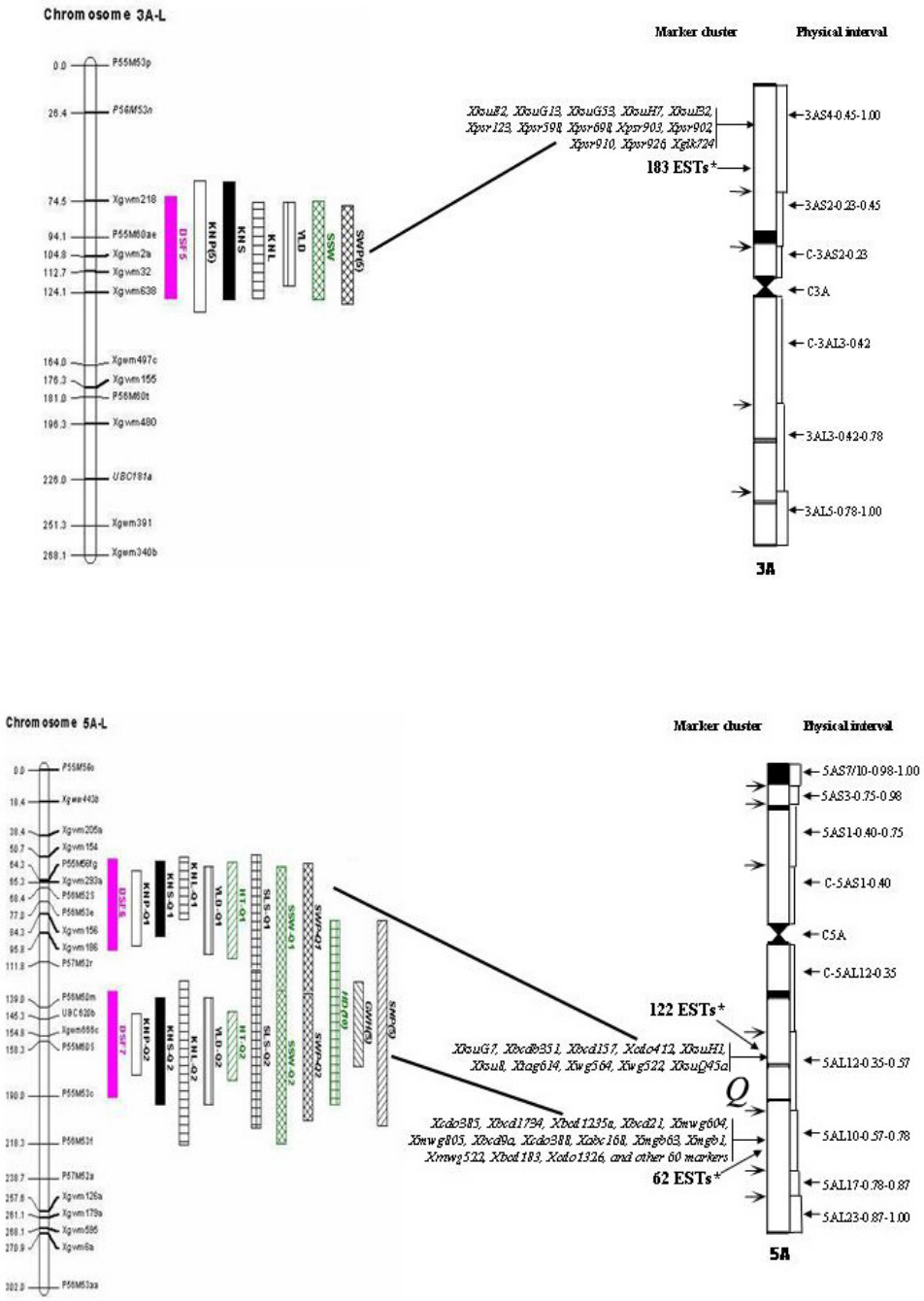

Figure 5 Continued.

production (Nevo, 2009). Wheat evolution studies showed that hexaploid bread wheat is derived from a spontaneous hybridization between tetraploid wheat and the diploid D genome donor, *Ae. tauchii*, and doesn't have a wild hexaploid progenitor (Kihara, 1944; McFadden and Sears, 1946; Kerber, 1964; Kislev, 1980; Dvorak et al., 1998a; Matsuoka and Nasuda, 2004). Thus, the wheat domestication process mainly occurred in tetraploid wild emmer wheat (*T. dicoccoides*) containing A^uA^uBB genomes. The A^u genome in bread and durum wheat is different from A^m in *T. boeoticum* but the same as in *T. dicoccoides*. Therefore, the wild emmer wheat, *T. dicoccoides*, actually is the core in wheat domestication evolution. The earliest present evidence for wheat utilization is from Ohalo, a site near the Lake of Galilee where a 19,000-year-old wild emmer wheat, *T. dicoccoides,* with brittle rachis was found, permitting sedentism and cereal agriculture (Kislev et al., 1992). However, wild emmer was first cultivated in the southern Levant in the Pre-Pottery Neolithic A (PPNA) 10,300-9,500 BP. Domesticated emmer (with a *non-brittle* rachis) appeared several hundred years later in the late PPNB (9,500-9,000 BP), which was grown mixed with wild emmer in many Levantine sites. Types with naked free-threshing grains emerged in the late PPNB (9,000-7,500 BP) (Feldman and Kislev, 2007). Mutations affecting spike traits including shattering, also called brittle rachis (controlled by genes *Br1* and *Br2*), tough glume (controlled by genes *Tg* and *Sog*), and speltoid spike (*q*, non-free threshing) were largely responsible for wheat domestication (Gill et al., 2007). Wild emmer wheat, *T. dicoccoides*, possesses important beneficial traits, stripe (yellow) -and stem rust resistance, powdery mildew resistance, soil born wheat mosaic virus, amino acid composition, grain protein content and storage protein genes (HMW glutenins), high photosynthetic yield, salt and drought tolerance, herbicide resistance, amylases and alpha amylase inhibitors, micronutrients such as Zn and Fe (Cakmak et al., 2004; Uauy et al., 2006), and genotypic variation for diverse traits as germination, biomass, earliness, nitrogen content, and yield, short stature, and high tillering capacity (Nevo et al., 2002). However, *T. dicoccoides* also shows agriculturally deleterious features such as brittle rachis; no-free-threshing characteristic; few, small, and light spikes; and small grains. Nevertheless, among the 75 domestication QTL effects for 11 traits, wild QTL alleles of *T. dicoccoides* for 18 (24%) effects were agriculturally beneficial, e.g., contributing to short plant, early HD, more spike number/plant, higher spike weight/plant, more kernel number per spikelet, higher GWH, and higher yield. Thus, this large portion of cryptic beneficial alleles together with genes for resistance or tolerance to biotic and abiotic stresses and high protein content (Nevo et al., 2002) could substantially advance the utilization of *T. dicoccoides* for wheat improvement (Xie and Nevo, 2008; Gustafson et al., 2009; Nevo and Chen, 2010; Krugman et al., 2010). As of today much of the adaptive vast potential genetic resources existing in wild emmer remains to be tapped and exploited for wheat improvement.

Concluding remarks and future perspectives

During agricultural development, early domesticates were gradually replaced first by landraces and traditional varieties, and later by genetically less-diverse modern cultivars. This has resulted in genetic bottlenecks and loss of diversity in breeding germplasm (Tanksley and McCouch, 1997; Nevo, 2004; Fu and Somers, 2009). Though experiencing the diversity bottlenecks, wheat has strong adaptability to diverse environments and end uses. Wheat compensates for these bottlenecks by capturing part of the genetic diversity of its progenitors and by generating new diversity at a relatively fast pace (Dubcovsky and Dvorak, 2007). Therefore, germplasm collections are essential to conserve biodiversity and thus pay big dividends to agriculture when used efficiently (Nevo, 1983, 1986, 1989, 1995, 1998, 2001, 2004, 2007, 2009, 2010; Xie and Nevo, 2008; Nevo and Chen, 2010; Johnson, 2008). Wild emmer wheat, *T. dicoccoides*, is the progenitor of cultivated wheats, has the same genome formula as durum wheat and has contributed two genomes to bread wheat that contains three genomes, and is central to wheat domestication. This wheat progenitor should be subjected to in-depth studies to evaluate its structural, functional, and regulatory polymorphisms adapting it to environmental stresses (Nevo, 2004; Parsons, 2005). The available crop genome sequences and undergoing genome sequencing of wheat can transform today's biology (Schuster, 2008), dramatically advancing both theory and application of wheat domestication study. The relationship between genomic and epigenomic diversities (Kashkush et al., 2002; Levy and Feldman, 2004; Kashkush, 2007) could be highlighted by deciphering the regulatory function of noncoding genomes on genic components. Regulation in particular might be the key in future domestication studies. It might decipher both speciation and adaptation processes to stressful, heterogeneous, and changing environments. The *nonrandom* adaptive processes and complexes in wild emmer and other wheat relatives could provide the basis for wheat improvement as single genes, QTLs, and interacting biochemical networks. It is essential to follow domestication processes and unravel many functional and regulatory genes that were eliminated from the cultivars during domestication, primarily by modern breeding. Identifying the polycentric sites of wild emmer domestication in the southern Levant versus monocentric ideas is feasible by tracking non-brittle rachis remains during initial phases of the "agricultural revolution", which may have been a gradual rather than a revolutionary process. This future research could identify lost adaptive genes during domestication and their active introgression from wild emmer back to cultivated wheat for genetic reinforcement (Nevo, 2010). Whole genomes of several crops including rice, maize, and sorghum have been sequenced, and the sequences have proved to be useful in domestication genomics studies. The sequence data can be used to study the origin of genes and gene families, track rates of sequence divergence over time, and provide hints about how genes evolve and generate products with novel biological properties (Hancock, 2005). However, wheat genome sequencing is still in its infant stage due to its huge genome size. Nevertheless, physical mapping and sequencing of the wheat genome (Feuillet and Eversole, 2007) have being conducted by the International Wheat Genome Sequencing Consortium (IWGSC) and other research institutions since 2005. Physical maps are mandatory for the development of whole genome reference sequences of large and complex genomes, such as those of the Triticeae crop species wheat, barley, and rye (Stein, 2009). A bacterial artificial chromosome (BAC)–based integrated physical map of the largest wheat chromosome 3B (995 megabases) was constructed recently (Paux et al., 2008). This physical map establishes a template for the remaining wheat chromosomes and demonstrates the feasibility of constructing physical maps in large, complex, polyploidy genomes with a chromosome-based approach. These efforts develop the needed background for sequencing the hexaploid and diploid wheat genomes and provide theoretical evolutionary perspectives and excellent tools for wheat domestication studies and for optimizing breeding practices (Feuillet and Eversole, 2007). This is a long-term, milestone-based strategy that delivers products and tools while working towards the ultimate goal of enabling profitability

throughout the industry. It involves the following perspectives: (1) physical mapping of bread and diploid wheat genomes; (2) genome sequencing launching pad; (3) robust bioinformatics platform; and (4) whole genome enabled functional genomics. Twenty countries and more than 200 members participate in this heroic effort to sequence the ~17,000 Mb bread wheat genome with its ~85% repeat sequences, which is 120-fold of the *A. thaliana* genome and 45-fold of rice and *Brachyopodium* genomes. Clearly, wheat represents a challenge for genomic studies and sequencing. Recently, increased marker density and genome sequencing of several cereal genomes revealed detailed intragenomic colinearity enabling the identification of paleo-duplications and propose a model of grass genome from a common ancestor. On the basis of five ancestral chromosomes, the "inner circle" was defined as providing new insights into the origin of evolution of grasses (Bolot et al., 2009). Upon completion of genome sequencing of either diploid wild wheat, *T. urartu* or *Ae. tauschii*, or hexaploid bread wheat, *T. aestivum*, domestication syndrome factors and other relevant genes and QTLs could be isolated, and effects of wheat domestication would be accurately estimated. The improvement of bread wheat is a future challenge of mankind, based on the evidence and ideas presented above and much earlier presented by Aaronshon and Schwinfurth (1906) and Aaronshon (1910), based on the distinct adaptive complexes of *T. dicoccoides* to environmental stress and their direct relevance to wheat domestication.

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