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REVIEW

Domestication evolution, genetics and genomics in wheat

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Abstract Domestication of plants and animals is the major factor underlying human civilization and is a gigantic evolutionary experiment of adaptation and speciation, generating incipient species. Wheat is one of the most important grain crops in the world, and consists mainly of 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%. In this review, we summarize and discuss research on wheat domestication, mainly focusing on recent findings in genetics and genomics studies. *T. aestivum* originated from a cross between domesticated emmer wheat *T. dicoccum* and the goat grass *Aegilops tauschii*, most probably in the south and west of the Caspian Sea about 9,000 years ago. Wild emmer wheat has the same genome formula as durum wheat and has contributed two genomes to bread wheat, and is central to wheat domestication. 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 involves a limited number of chromosome regions, or domestication syndrome factors, though many relevant quantitative trait loci have been detected. On completion of the genome sequencing of diploid wild wheat (*T. urartu* or *Ae. tauschii*), domestication syndrome factors and other relevant genes could be isolated, and effects of wheat domestication could be determined. The achievements of domestication genetics and robust research programs in Triticeae genomics are of greatly help in conservation and exploitation of wheat germplasm and genetic improvement of wheat cultivars.

Keywords Cultivated wheat · Wild emmer wheat · Evolution and domestication · Major domestication gene · Domestication-related QTL · Domestication syndrome factor

Abbreviations

Mya	Million years ago
BP	Years before present
SSR	Simple sequence repeat

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Br	Brittle rachis
Tg	Tenacious glume
Ppd	Photoperiod response
QTL	Quantitative trait locus
DSF	Domestication syndrome factor
AFLP	Amplified fragment length polymorphism

Introduction

Domestication is the outcome of a selection process that results in the increased adaptation of plants or animals to cultivation or rearing and use by humans (Brown 2010). It is a gigantic evolutionary experiment of adaptation and speciation, generating incipient species (Darwin 1905). It has been performed by humans primarily during the last 10,000 years (Zohary and Hopf 2000; Feldman and Kislev 2007), and has led to adaptive syndromes fitting human ecology (Harlan 1992). Human sedentism, urbanization, culture and an unprecedented population explosion have depended, to a large extent, on domestication and the related agricultural economies. Human behaviours and plant genetic adaptations have been entangled during the domestication (Allaby 2010; Fuller et al. 2010). Domestication makes all the cultivars, including wheat, human-dependent, capable of surviving only under cultivation in human agricultural niches to meet human needs (Gustafson et al. 2009; Nevo 2011).

Wheat is the universal cereal of Old World agriculture (Zohary and Hopf 2000) and the world's foremost crop plant (Feldman et al. 1995; Gustafson et al. 2009), followed by rice and maize. Modern wheat cultivars usually refer to two species: hexaploid bread wheat, *Triticum aestivum* ($2n = 6x = 42$, A^uA^uBBDD), and tetraploid, hard or durum-type wheat, *T. durum* ($2n = 4x = 28$, A^uA^uBB) 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, and durum wheat the other 5%. Today, wheat ranks first in world grain production and accounts for more than 20% of total human food calories. Wheat is extensively grown on 17% of all crop areas, in the temperate, Mediterranean-type and subtropical parts of both hemispheres, from 67°N in Norway, Finland and Russia to 45°S in Argentina. It is the staple food for 40% of the world's population, mainly in Europe, North America and the western and northern parts of Asia (http://www.faostat.fao.org; http://www.croptrust.org).

Wheat is a superb model organism for the evolutionary theory of allopolyploid speciation, adaptation and domestication in plants (Gustafson et al. 2009). Its domestication caused substantial genetic erosion and that erosion was reinforced during modern breeding processes, and thus increased susceptibility and vulnerability to environmental stresses, pests and diseases (Nevo 2009, 2011; 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, wild emmer *T. dicoccoides* and other wheat relatives (Feldman and Sears 1981; Nevo and Beiles 1989; Nevo et al. 2002; Nevo 2011).

The economic importance of wheat has triggered intense cytogenetic and genetic studies in the past decades that have resulted in a wealth of information and tools which have been used to develop wheat cultivars with increased yield, improved quality and enhanced biotic and abiotic stress tolerance (Carver 2009). In contrast, genomics in wheat has lagged behind other plant species, and is hampered by the huge genome sizes (15,961 Mb for bread wheat; 11,660 Mb for durum wheat; Bennett and Leitch 2010) and complexity of the genomes. Recently, however, the situation has changed dramatically and the convergence of several technological developments has led to the development of new and more efficient resources that support the establishment of robust genomic programs in wheat (Feuillet and Muehlbauer 2009). These new capabilities will provide a better understanding of wheat domestication evolution and support the improvement of agronomically important traits in this essential species (Feuillet and Muehlbauer 2009; Paux and Sourdille 2009). Therefore, we are currently witnessing a pinnacle of genomic research into the process of domestication itself, particularly the specific major and minor genes involved (Brown 2010), and the epic effort to sequence the wheat genome. In this review we summarize and discuss the most recent

achievements of wheat domestication studies, especially in the fields of genetics and genomics.

Evolution of wheat

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 diverged around 20 Mya (Inda et al. 2008). Wild diploid wheat (*T. urartu*, $2n = 2x = 14$, genome A^uA^u) hybridized with the B genome ancestor that is the closest relative of goat grass (*Aegilops speltoides*, $2n = 2x = 14$, genome SS) 300,000–500,000 years before present (BP) (Huang et al. 2002; Dvorak and Akhunov 2005) to produce wild emmer wheat (*T. dicoccoides*, $2n = 4x = 28$, genome A^uA^uBB). 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 et al. (2004) presented evidence for grain processing and baking of flour. About 10,000 BP, hunter-gatherers began to cultivate wild emmer. Subconscious selection gradually created a cultivated emmer (*T. dicoccum*, $2n = 4x = 28$, genome A^uA^uBB) 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 A^uA^uBBDD) (http://www.newhallmill.org.uk/wht-evol.htm; Kihara 1944; McFadden and Sears 1946; Kerber 1964; Kislev 1980; Dvorak et al. 1998; Matsuoka and Nasuda 2004). This cross took place after emmer wheat cultivation expanded eastwards from the Fertile Crescent to the natural habitat of *Ae. tauschii*, and occurred probably south and west of the Caspian Sea (Nesbitt and Samuel 1996; Salamini et al. 2002; Giles and Brown 2006). 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*) and bread wheat (*T. aestivum*) (Fig. 1). However, recent experimental evidence suggests that *T. spelta* is not the ancestral form of free-threshing common wheat (Dvorak et al. 2006). Apparently, the sources of cultivated wheat ancestry are complicated by multiple factors including gene flow from wild cereals (Dvorak et al. 2011).

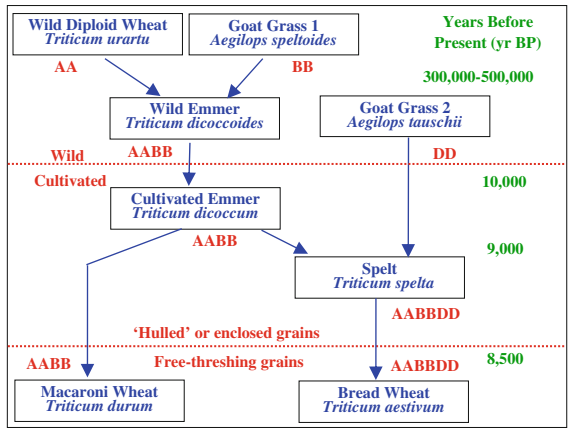


Fig. 1 The evolution of wheat from the prehistoric Stone Age grasses to modern macaroni wheat and bread wheat (reproduced from http://www.newhallmill.org.uk/wht-evol.htm)

Domestication of wheat

According to the history of wheat evolution described above, only wild einkorn and wild emmer wheats were subjected to domestication selection. The hexaploid common or bread wheat was not directly derived from a wild progenitor through domestication selection but from *T. turgidum* spp. *dicoccon* (Dvorak et al. 2011). Therefore, we only review here the domestication studies on diploid einkorn wheat and tetraploid emmer wheat.

There are two wild diploid *Triticum* species recognized: *T. boeoticum* (A^bA^b) and *T. urartu* (A^uA^u). They have crossing barriers between them (Johnson and Dhaliwal 1976) and differ in plant morphology (Gandilian 1972; Dorofeev et al. 1979) and at biochemical and molecular marker loci (Johnson 1975; Dvorak et al. 1998, 2011; Kilian et al. 2007). The diploid einkorn wheat *T. monococcum* was one of the first crops domesticated in the Fertile Crescent from the wild progenitor species *T. boeoticum*. The domestication of einkorn wheat occurred in the Karacadag mountain range in southeast Turkey (Heun et al. 1997). During the last 5,000 years, einkorn was basically replaced by tetraploid and hexaploid wheats. Einkorn is currently a relict crop and is only grown on a very small scale as

feed in a few Mediterranean countries (Nesbitt and Samuel 1996; Perrino et al. 1996).

The other wild diploid *Triticum* species, *T. urartu* (A^uA^u), occurs in parts of the Fertile Crescent (Zohary and Hopf 2000), and has played an essential role in wheat evolution though it has never been domesticated. *T. urartu* contributed the A^u genome to all tetraploid and hexaploid wheats (Dvorak et al. 1993). There are also two wild tetraploid wheat species known as *T. dicoccoides* (A^uA^uBB) and *T. araraticum* (A^uA^uGG). Tests using DNA molecular markers show that wild tetraploid wheat did participate in the evolution of hexaploid wheat (Dvorak et al. 2011). *T. dicoccoides*, wild emmer, grows naturally all over the Fertile Crescent. Wild emmer wheat was discovered in 1906 by Aaron Aaronsohn in Israel (Aaronsohn and Schweinfurth 1906). The domesticated form of *T. dicoccoides* is known as *T. dicoccum* (emmer, A^uA^uBB).

Emmer is believed to have been domesticated probably in southeast Turkey (Özkan et al. 2002, 2005, 2010; Mori et al. 2003; Luo et al. 2007; Dvorak et al. 2011). 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 (Özkan et al. 2002, 2010; 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. Based on geographical distribution and molecular marker data, Özkan et al. (2010) most recently suggested that the "dispersed-specific" domestication model proposed for einkorn might appropriately fit emmer. The model assumes pre-adaptation of a wild emmer race for cultivation. This race was spread to several locations in the Fertile Crescent before being domesticated at several sites.

However, the allozymic study of Nevo and Beiles (1989) found no evidence for two races of *T. dicoccoides*. Archaeological findings from the period of 10,300–9,500 BP shows that wild emmer was first cultivated in the southern Levant. Domesticated emmer appeared several hundred years later, i.e., 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 during the period 9,000–7,500 BP. These archaeological findings of wild emmer cultivation and domestication do not support the hypothesis of domestication within a small core area, but rather demonstrate the polycentric origin of agriculture in the Levant (Kislev et al. 1992; Feldman and Kislev 2007). As reviewed most recently by Özkan et al. (2010), archaeobotanical studies strongly suggest that wild emmer was possibly twice and independently taken into cultivation, in the southern Levant and in the northern Levant. The model of multiple-site independent domestication of wild emmer across the Levant seems more realistic. According to this model, the genes for non-brittleness were transferred to numerous wild emmer genotypes through numerous spontaneous hybridizations and spontaneous mutations, followed by human selection. Consequently, domesticated emmer wheat evolved as polymorphic populations rather than as single genotypes (Feldman and Kislev 2007). Domesticated emmer was once the main crop for bread-making in ancient Egypt. Emmer cultivation has significantly declined and can be found only in a few traditional farming communities, mainly in Russia and Ethiopia. Durum wheat (*T. durum*) derived from *T. dicoccum* (Damania 1998) is a free-threshing naked wheat and is widely cultivated today for pasta production.

Speed of wheat domestication

Conventionally, wheat domestication studies have focused on a few qualitative traits (brittle rachis, tough glume and free-threshing) controlled by single major genes (Br/br, Tg/tg and Q/q; see Fig. 2 and Gill et al. 2007). 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 practices and concluded that perhaps only 20–30 years would be enough to completely domesticate these plants. Honne and Heun (2009) validated this viewpoint.

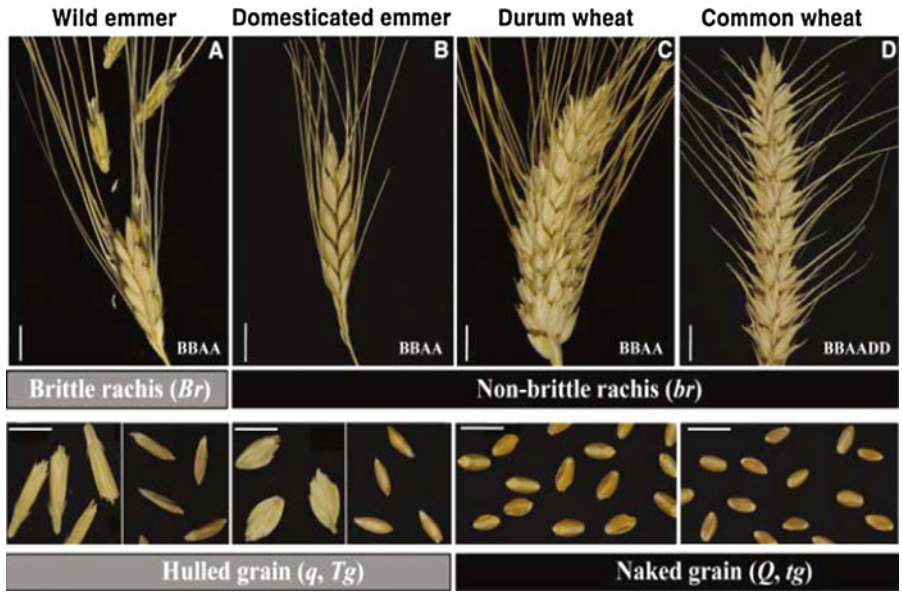


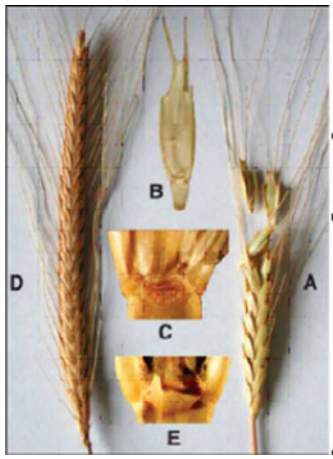
Fig. 2 Wheat spikes showing **a** brittle rachis, (**b** to **d**) non-brittle rachis, (**a** and **b**) hulled grain, and (**c** and **d**) naked grain. **a** Wild emmer wheat (*T. dicoccoides*), **b** domesticated emmer (*T. dicoccum*), **c** durum (*T. durum*), and **d** common wheat (*T. aestivum*). *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 (reproduced from Dubcovsky and Dvorak 2007)

However, the fact that remains of wild and domesticated forms of the same plant overlapping for a long time (up to 3,000 years) is inconsistent with rapid domestication (Tanno and Willcox 2006; Balter 2007; Willcox et al. 2008). Indehiscence took over one millennium to become an established event (Tanno and Willcox 2006, Fig. 3). This means that early farmers possibly did not focus only on indehiscence, but also on other important quantitative traits—spike size, heading date/growth duration, plant height, grain size, etc.—in the harvesting process of wild wheat. Measurements taken from ancient grains demonstrate that the size of wheat and barley grains remained essentially the same between 9,500 and 6,500 BP (Willcox 2004). Therefore, selection for large cereal grains was slow because grain size was controlled by polygenes (Peng et al. 2003).

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 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 (Feldman and Kislev 2007), during which wild wheat persisted in cultivated fields. Therefore, the process of wheat domestication was slow, spanned over one thousand years, occurred in multiple sites of the Fertile Crescent, and fitted a gradualist and multi-site model (Fig. 3, Tanno and Willcox 2006; Feldman and Kislev 2007). This multi-site and long-term domestication seems more realistic than the fast domestication.

Effects of domestication on genetic diversity

Domestication of plants and animals usually results in a reduction of genetic diversity involving the whole genome (Doebley 1989; Gepts 2004; Ross-Ibarra et al. 2007; Fu and Somers 2009). The domesticate acquires improved fitness for human purpose often at the expense of survival in nature, and a mutualistic relationship evolves between humans and their crops through the domestication process (Gepts 2004). One of the correlated changes in the genome is consequential phenomena, such as loss of diversity, selective sweeps and adaptive diversification (Brown 2010). The bottleneck reduces diversity in neutral genes, but selection decreases diversity beyond that caused by the bottleneck alone (Ross-Ibarra et al. 2007). Several demographic and selective events occurred during the domestication of wheat from *T. dicoccoides*. Haudry et al. (2007) analyzed



F

Dates (year BP)	Archaeological site	Domestication rate (%)
10,200	Qaramel	22
9,250	Nevali Cori	32
9,300-8,500	Aswad	30
8,500-7,500	Ramad	59
7,500	el Kerkh	59
6,500	Kosak Shamali	95

Fig. 3 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 table (*f*) gives relative frequencies of sub-fossil finds. Records from Aswad and Ramad (van Zeist and Bakker-Heeres 1985) are of barley; the other four sites are of wheat (reproduced from Tanno and Willcox 2006)

nucleotide diversity at 21 loci in wild and domesticated, cultivated durum and bread wheats, and revealed that diversity was further reduced in cultivated forms during domestication—by 69% in bread wheat and 84% in durum wheat.

Demographic events can have dramatic effects on the long-term effective size (*Ne*) of a population. Reductions of *Ne*, typically referred to as genetic bottlenecks, have usually led to decreased levels of diversity in cultivated crops relative to their wild progenitors (Buckler et al. 2001). Using simple sequence repeat (SSR) marker data, Thuillet et al. (2005) found a *Ne* of 32,500 individuals in wild emmer wheat, 12,000 in the domesticated form, 6,000 in landraces and 1,300 in recent improved varieties of tetraploid wheat. This decrease clearly demonstrates the successive bottlenecks in durum wheat during domestication and subsequent agronomic improvement of the species.

Dubcovsky and Dvorak (2007) believe that high mutation rates, together with buffering effects caused by polyploidy, should enable hexaploid wheat to enhance diversity. However, a genome-wide examination of 75 Canadian wheat (*T. aestivum*) cultivars released from 1845 to 2004 examined by using 370 SSR markers indicated that allelic reduction occurred in every part of the wheat genome and a majority of the reduced alleles resided in only a few early cultivars. The net reduction of the total SSR variation in 20 recent cultivars was 17% (Fu and Somers 2009). Based on a large-scale single nucleotide polymorphism (SNP) analysis in wheat, Akhunov et al. (2010) suggest that ancestral species are the primary source of genetic diversity in the young polyploidy species, *T. aestivum*. Low effective recombination resulting from self-pollination and a genetic mechanism prohibiting homeologous chromosome pairing during meiosis can cause diversity loss in large chromosomal regions. Accumulation of new mutations in older polyploid species, such as wild emmer, results in increased diversity and its more uniform distribution across the genome (Akhunov et al. 2010). Based on the haplotype analysis of a dimorphism locus (*ABCT-A1a/b*), Dvorak et al. (2006) believe that *T. aestivum* in eastern Asia conserved the gene pool of the original *T. aestivum* more than wheat elsewhere, and diffusion of the original *T. aestivum* from Transcaucasia or the southwestern Caspian westward to eastern Turkey would have resulted in sympatry with wild emmer and potential for gene flow from wild emmer to *T. aestivum*. Such gene flow unavoidably increased genetic diversity in *T. aestivum*, and modified the geographical pattern of wheat genetic diversity (Dvorak et al. 2011). Analyses of linkage disequilibrium (LD) and SNP variation have showed that breeding and selection had a different impact on each wheat genome both within and among populations, and revealed the highest extent of significant LD in the wheat D-genome, which likely reflects the

episodes of recent introgression and population bottleneck accompanying the origin of hexaploid wheat (Chao et al. 2010). Therefore, modern breeding does reinforce the genetic bottlenecks which started with early domestication of wheat, but the dominant mechanism of chromosome number reduction caused by inversions and translocations in grasses could have accelerated genome evolution in the polyploid Triticeae (Luo et al. 2009), and it is vital to conserve wheat germplasm and introduce genetic diversity into wheat breeding programs from both landraces and wild relatives.

Genetic and genomic dissection of qualitative domestication traits

Recent genetic and genomic studies are summarized for the following qualitative traits that have undergone domestication selection in wheat.

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 symbol 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 (Zohary and Hopfs 2000). 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). In a cross between semi-wild wheat and *T. 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. spelta*, *T. macha* and *T. 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 one tough rachis in the F2 progeny of wild × domesticated crosses (Sharma and Waynes 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). This major distinguishing feature, brittle rachis, 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 (Cao et al. 1997; Chen et al. 1998; Watanabe and Ikebata 2000; Nalam et al. 2006; Gill et al. 2007).

The previous studies show (1) multiple genetic pathways controlling the trait(s); and (2) different genetic origins of loci controlling shattering in polyploids (Salamini et al. 2002). These considerations, combined with the mapping of quantitative trait loci (QTL) for shattering, allow analyses of the microsyntenous relationships between 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 free-threshing habit and is modified by the domestication process in wheat (Gill et al. 2007). The wild 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 over 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 between semi-wild wheat and *T. spelta*, the F2 and F3 populations 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 control the free-threshing trait in crosses involving synthetic wheats (Villareal et al. 1996). Jantasuriyarat et al. (2004) detected several QTL 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 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 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 different 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*) and hexaploid bread wheat (*T. aestivum*), 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; Gill et al. 2007). 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 one to five 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*.

The *Tg* gene controls the speltoid phenotype and inhibits the expression of *Q*. The suppression of the free-threshing character is thought to be due to a partially dominant *Tg* allele on chromosome 2D, derived from *Ae. tauschii* and thus resulting in tenacious glumes. The conclusion is that free-threshing hexaploids have the genotype *tgtg*, *QQ* (Kerber and Rowland 1974; Villareal et al. 1996; see Fig. 2).

In general, the *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). Faris et al. (2005) and Gill et al. (2007) cloned the *Q* gene and unravelled 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, and is 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 those 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.

Genetic and genomic analysis of quantitative domestication traits

Additional traits modified during domestication and the subsequent breeding process are quantitatively inherited: e.g., grain yield, seed size, plant height and heading date (Table 1). Furthermore, the spread of domesticated wheat from the Fertile Crescent required 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, is under complex polygenic control, and the genes have been mapped to seven or eight chromosomes (Table 1, Elias et al. 1996; Peng et al. 2003; Gegas et al. 2010). The major seed-size QTL correspond closely in sorghum, rice and maize, and other QTL 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 seed-size QTL detected in *T. dicoccoides* correspond to their rice counterparts (Peng et al. 2003).

Flowering time

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/flowering time is an important criterion for regional adaptation in all cereals. The control of heading date is critical for reproductive success and

Table 1 Quantitative trait loci related to domestication in wheat

Trait	Number of QTL effects	Residing chromosome[a]	Reference
Seed size/weight	7	1A, 2A, 3A, 4A, 7A, 5B, 7B	Elias et al. (1996)
	8	1B, 2A, 4A, 5A, 5B, 6B, 7A, 7B	Peng et al. (2003)
	8	1B, 2A, 3A, 3B, 4B, 5A, 6A, 7A	Gegas et al. (2010)
Flowering time	4	2A, 4B, 5A, 6B	Peng et al. (2003)
Grain yield	8	**1B**, **2A**, 3A, **5A**, 5B	Peng et al. (2003)
	3	3A, 4A, 5A	Araki et al. (1999), Shah et al. (1999), Kato et al. (2000), Campbell et al. (2003)
Plant height	4	**5A**, **7B**	Peng et al. (2003)
Spike number/plant	7	**1B**, 2A, 2B, 5A, **7A**	Peng et al. (2003)
Spike weight/plant	10	**1B**, **2A**, 3A, **5A**, 5B, **7A**	Peng et al. (2003)
Single spike weight	5	1B, 2A, 3A, **5A**	Peng et al. (2003)
Kernel number/plant	9	**1B**, **2A**, 3A, **5A**, 5B, 7A	Peng et al. (2003)
Kernel number/spike	7	1B, **2A**, 3A, **5A**, 6B	Peng et al. (2003)
Kernel number/spikelet	7	1B, 2A, 3A, **5A**, 5B, 7B	Peng et al. (2003)
Spikelet number/spike	6	1B, 2A, **5A**, **6B**	Peng et al. (2003)

[a] The bold-font chromosome carry a pair of linked QTL

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 a different response to long days. Reduced photoperiod response is important in Europe and North America, where growing seasons are long (Turner et al. 2005). Four heading date QTL located on four chromosomes were identified (Table 1). The wild allele for the QTL on 5A increases the value of heading date and so is responsible for the late flowering of *T. dicoccoides*, whereas the wild heading-date alleles on other chromosomes can accelerate the flowering date (Peng et al. 2003).

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. 2007, 2009). On the basis of the map positions, it can be postulated that the heading date QTL on 5A (Fig. 4) may be similar to the *VRN1* gene mapped on chromosome 5A in *T. monococcum*. 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 heading date 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. Major photoperiod-related genes/gene families are conserved between barley and *Arabidopsis*, involving the GI, CO and 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). However, these grass QTL did not associate with flowering time but co-segregate with orthologous *Arabidopsis* "flowering" genes. Therefore, different major determinants of photoperiod have been selected in the Triticeae (Börner et al. 1998; Griffiths et al. 2003).

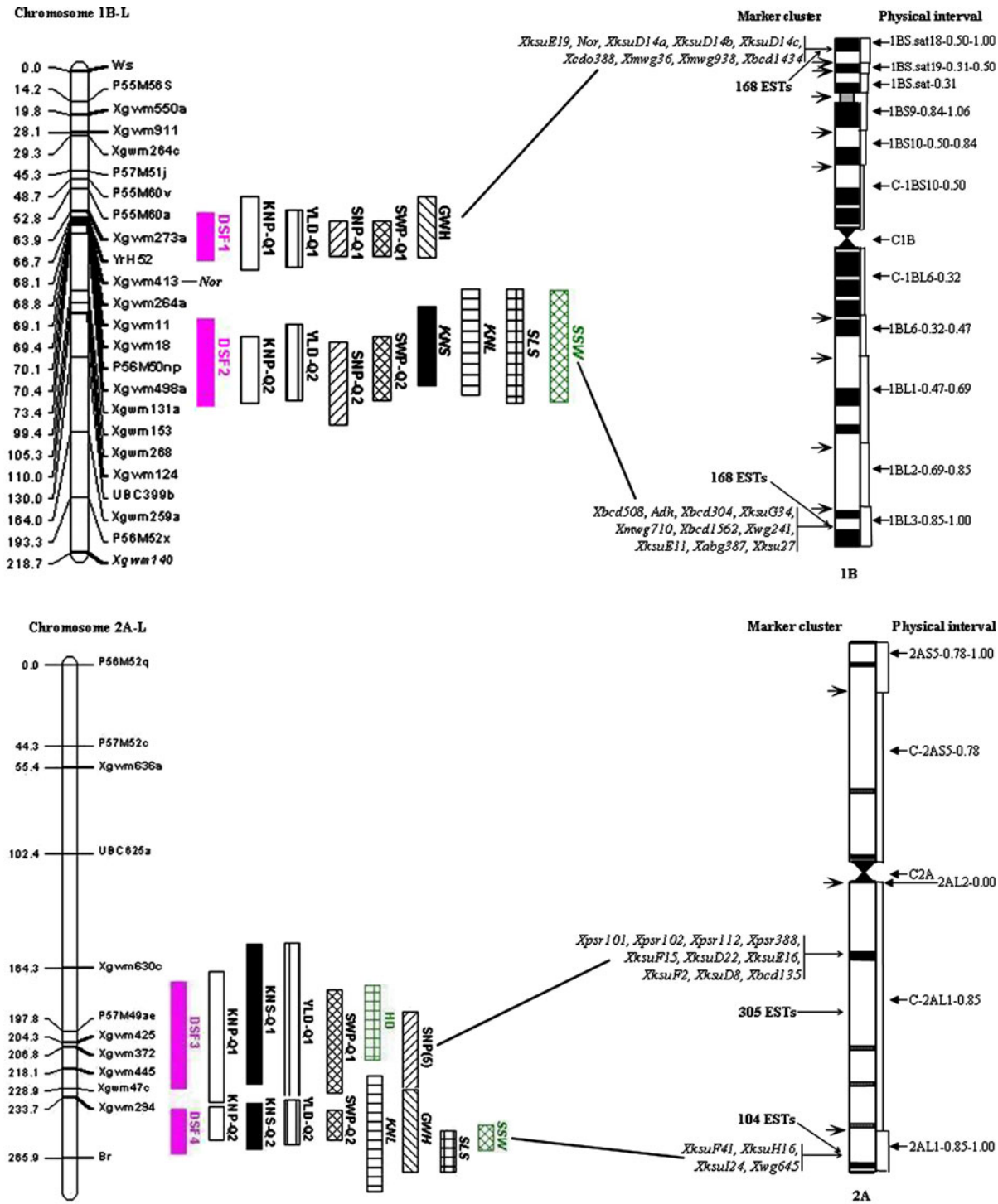
Fig. 4 Map and physical locations of DSFs and their involved QTLs in L version maps of wild emmer wheat, *T. dicoccoides*. Genetic map is on the left-hand side, and the right-hand side is the physical bin map. Short arms of chromosomes are at the top. The domestication syndrome factors and the corresponding QTLs are shown on the right-hand side of the map: DSF, domestication syndrome factor; KNS, kernel number/spike; KNL, kernel number/spikelet; YLD, grain yield/plant; HT, plant height; SLS, spikelet number/spike; SSW, single spike weight; SWP, spike weight/plant; KNP, kernel number/plant; HD, heading date; GWH, grain weight; SNP, spike number/plant. 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%. (Reproduced from Peng et al. 2003) ▶

Grain yield and other traits

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. Using an advanced QTL mapping software, MultiQTL (http://www.multiqtl.com), eight yield QTL located in five chromosomes were identified (Table 1). The yield QTL overlapped with QTL for other traits (Fig. 4). QTL 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).

During the domestication process involving the qualitative and quantitative traits described above, many other quantitative traits were also co-selected by ancient farmers. These traits include plant height, spike number/plant, spike weight/plant, single spike weight, kernel number/plant, kernel number/spike, kernel number/spikelet and spikelet number/spike. Using MultiQTL mapping software, as many as 55 QTL effects were detected for these eight traits (Table 1).

Plant height is an extremely important target trait in modern wheat breeding since the "green revolution" in cereals was achieved by reducing plant height, and thus the lodging susceptibility and increase in grain yield (Hedden 2003). However, dwarf wheat cultivars were used only in commercial


Chromosome 1B-L
Marker cluster
Physical interval
0.0 Ws
14.2 P55M56 S
19.8 Xgwm550a
28.1 Xgwm911
29.3 Xgwm264c
45.3 P57M51j
48.7 P55M60v
52.8 P55M60a
63.9 Xgwm273a
66.7 YrH52
68.1 Xgwm413 — Nor
68.8 Xgwm264a
69.1 Xgwm11
69.4 Xgwm18
70.1 P56M50np
70.4 Xgwm498a
73.4 Xgwm131a
99.4 Xgwm153
105.3 Xgwm268
110.0 Xgwm124
130.0 UBC399b
164.0 Xgwm259a
193.3 P56M52x
218.7 Xgwm140
DSF1
DSF2
KNP-Q1
KNP-Q2
YLD-Q1
YLD-Q2
SNP-Q1
SNP-Q2
SWP-Q1
SWP-Q2
GWH
KWS
KWL
SLS
SSM
XksuE19, Nor, XksuD14a, XksuD14b, XksuD14c, Xcdo388, Xmwg36, Xmwg938, Xbcd1434
168 ESTs
1BS.sat18-0.50-1.00
1BS.sat19-0.31-0.50
1BS.sat-0.31
1BS9-0.84-1.06
1BS10-0.50-0.84
C-1BS10-0.50
C1B
C-1BL6-0.32
1BL6-0.32-0.47
1BL1-0.47-0.69
1BL2-0.69-0.85
168 ESTs
Xbcd508, Adh, Xbcd304, XksuG34, Xmwg710, Xbcd1562, Xwg241, XksuE11, Xabg387, Xksu27
1BL3-0.85-1.00
1B
Chromosome 2A-L
Marker cluster
Physical interval
0.0 P56M52q
44.3 P57M52c
55.4 Xgwm636a
102.4 UBC625a
164.3 Xgwm630c
197.8 P57M49ae
204.3 Xgwm425
206.8 Xgwm372
218.1 Xgwm445
228.9 Xgwm47c
233.7 Xgwm294
265.9 Br
DSF3
DSF4
KNP-Q1
KNP-Q2
KNS-Q1
KNS-Q2
YLD-Q1
YLD-Q2
SNP-Q1
SWP-Q1
SWP-Q2
HD
SNP(6)
GWH
KWL
SLS
SSM
Xpsr101, Xpsr102, Xpsr112, Xpsr388, XksuF15, XksuD22, XksuE16, XksuF2, XksuD8, Xbcd135
305 ESTs
104 ESTs
XksuF41, XksuH16, Xksu124, Xwg645
2AS5-0.78-1.00
C-2AS5-0.78
C2A
2AL2-0.00
C-2AL1-0.85
2AL1-0.85-1.00
2A

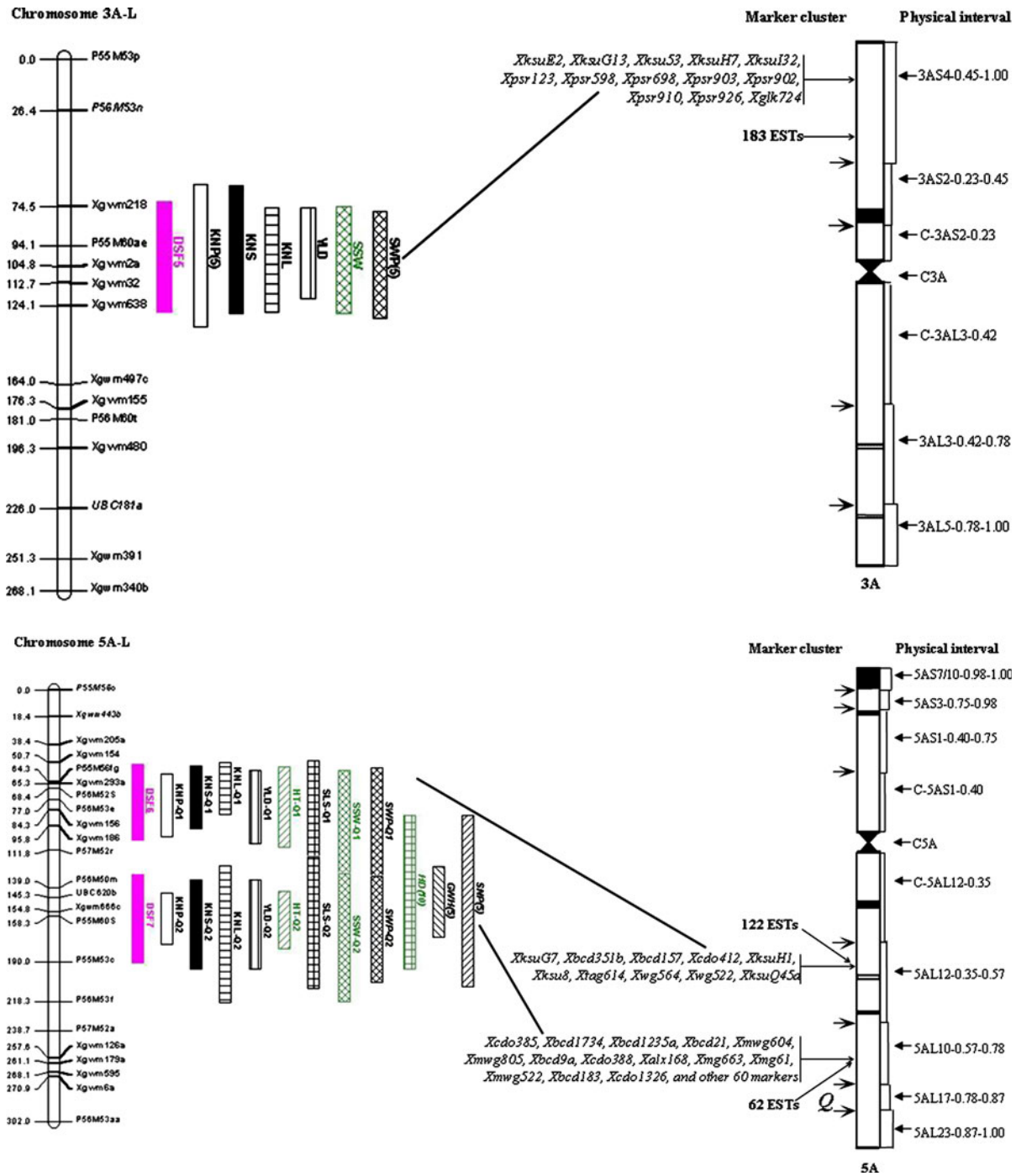


Fig. 4 continued

production after the 1960 s, and most of the wheat landraces are tall. Therefore, ancient farmers did not select the dwarf but selected the tall mutants that had higher biomass and yielding potential during domestication. Four QTL or two pairs of linked QTL for plant height were detected in chromosomes 5A and 7B (Table 1). One of the *T. dicoccoides* alleles on chromosome 5A was able to reduce plant height by 9.6–15.2 cm (Peng et al. 2003).

Spike number is one of the most important yield components and is highly correlated with tillering capacity in wheat. 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. Seven QTL effects for spike number were detected in five chromosomes (Table 1). A single recessive gene (*tin*) located on chromosome 1AS was found to control tiller number (Spielmeyer and Richards 2004). This gene is perhaps a homeologous 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 $3A^m$ (Kuraparthy et al. 2007, 2008).

Spike weight/plant and single spike weight are significantly correlated with each other, and also with grain weight/size and yield (Peng et al. 2003). Ten QTL effects were detected for spike weight/plant in six chromosomes, and five QTL effects were detected for single spike weight in four chromosomes (Table 1). Kernel number/plant, kernel number/spike, kernel number/spikelet and spikelet number/spike are highly correlated with each other and also with yield (Peng et al. 2003). Nine, seven, seven and six QTL effects were identified for kernel number/plant, kernel number/spike, kernel number/spikelet and spikelet number/spike, respectively (Table 1).

Among the chromosomes carrying domestication QTL, 5A harbours QTL effects for all the 11 traits examined, 2A carries QTL effects for 10 of the 11 traits, and 1B has QTL effects for 9 of the 11 traits (Table 1). Therefore, chromosomes 5A, 2A and 1B played key roles in domestication modification of these quantitative traits. Interestingly, the free-threshing gene *Q* discussed above is located in chromosome 5A (Luo et al. 2000). It is thus highly possible that the key domestication gene, *Q*, has pleiotropic effects on yield and yield components (Kato et al. 2003).

Domestication syndrome factors involving quantitative traits and gene-rich regions

Domesticated species differ from their wild ancestors and relatives in a set of traits that is known as the domestication syndrome. The most important syndrome traits include growth habit, flowering time, seed dispersal and gigantism (Frary and Doğanlar 2003). It would be very helpful for wheat breeding for high yield and good adaptability to understand the genomics/genetics of syndrome traits (Killian et al. 2009). Most of the significant QTL for domestication-related traits are clustered mainly in a limited number of intervals in chromosomes 1B, 2A, 3A and 5A (Fig. 4). Consequently, the total number of intervals carrying domestication QTL is 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). 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). This limited number of DSFs of wheat (Fig. 4) corroborates the results in other cereal crops, showing that the domestication syndrome is under a relatively simple and rapidly evolving genetic control (Paterson et al. 1995).

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. 1996a, b; Kunzel et al. 2000; Peng et al. 2004). The map positions of all seven wheat DSFs appear to overlap with gene-rich regions (Fig. 4) and the key domestication gene, *Q*. Therefore, the high pleiotropy and/or tight linkage of most wheat domestication QTL suggest an important role for recombination both in consolidation of positive mutations within the DSF clusters (Otto and Barton 1997) and 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. Dvorak (2009), however, pointed out that the evidence for gene-rich islands is weak. He proposed a model accounting for correlation between gene flow density and recombination rate. Furthermore, he also suggested that the vast numbers of repeated sequences in the Triticeae genomes (90% of the nuclear genomes) play a role in the evolution of new genes and in adaptation. The dramatic dynamics and evolution of adaptation and speciation of transposable elements (TEs) in diploid wheat has been described by Belyayev et al. (2010), and generally in Triticeae by Sabot and Schulman (2009).

Role of A and B genomes in wheat domestication

Inter-parental *Pst*I-based amplified fragment length polymorphisms (AFLPs) showed that molecular markers are nonrandomly distributed among the A and the 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, the numbers of both QTL effects and domestication syndrome factors in the A genome significantly exceeded those 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, the wheat A genome may have played a more important role than the B genome in the wheat domestication process. Gupta et al. (2008) believed that diploid wheat carrying the A genome was the first wheat to be domesticated, so that most of the domestication-related traits in different wheats must have been selected within the A genome. However, domestication is assumed to have occurred independently on tetraploid and diploid wild wheats. Therefore extensive and intensive phylogenetic analyses are needed to explain the fact that the A genome has played a stronger role than the B genome in the domestication process.

Importance of *Triticum dicoccoides* in wheat domestication and breeding

As reviewed above, hexaploid bread wheat is derived from a spontaneous hybridization between tetraploid wheat and the diploid D genome donor, *Ae. tauchii*. The wheat domestication events mainly occurred in diploid wheat (*T. boeoticum*) containing A^mA^m and tetraploid 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 central to wheat domestication evolution (Zohary and Hopf 2000; Nevo et al. 2002; Nevo 2011). Dvorak et al. (2006) conducted a deliberately designed analysis of genetics and genomics of wheat domestication, and showed for the first time that wild tetraploid wheat participated in the evolution of hexaploid wheat.

T. dicoccoides possesses important beneficial traits, e.g., resistance to stripe rust, stem rust, powdery mildew and 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 such as biomass, earliness, nitrogen content, 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 heading date, higher spike number/plant, higher spike weight/plant, higher kernel number per spikelet, higher GWH and higher yield (Peng et al. 2003). 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, Nevo 2011). To date, much of the vast potential adaptive genetic resources existing in wild emmer remains to be tapped and exploited for wheat improvement.

Conclusions and prospects

Wheat is one of the most important grain crops in the world. *T. dicoccoides*, the progenitor of cultivated wheats, is central to wheat domestication, fitting 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 actually restricted to a limited number of chromosome regions, or domestication syndrome factors. This finding is helpful for studies on genetics and genomics of wheat domestication. The physical mapping of polyploidy plant species (Fleury et al. 2010; Luo et al. 2010) and sequencing of the wheat genome initiated by the International Wheat Genome Sequencing Consortium (IWGSC) (Feuillet and Eversole 2007; Feuillet and Muehlbauer 2009) will further accelerate genomic studies on wheat domestication by providing powerful genomics tools. 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 diversity bottlenecks, wheat has strong adaptability to diverse environments and end uses due to the adaptive complexes that evolved in wild emmer in the near Fertile Crescent (Nevo et al. 2002). 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 2007, 2009, 2011; Nevo et al. 2002; Xie and Nevo 2008; Nevo and Chen 2010; Johnson 2008).

As a wheat progenitor, wild emmer wheat should be subjected to in-depth studies to evaluate the structural, functional and regulatory polymorphisms adapting it to environmental stresses (Nevo 2004; Parsons 2005). The available crop genome sequences and the current sequencing of the wheat genome can transform today's biology (Schuster 2008), dramatically advancing both the theory and application of wheat domestication studies. 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 (Li et al. 2002, 2003, 2004). 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 such as single genes, QTL 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 adaptive genes lost during domestication and enable their active introgression from wild emmer back to cultivated wheat for genetic reinforcement (Nevo 2011).

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 (Dvorak 2009). 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, Feuillet and Muehlbauer 2009). However, wheat genome sequencing is still in its infancy due to its huge genome size and the huge proportion of repetitive sequences (Dvorak 2009). Nevertheless, physical mapping and sequencing of the wheat genome (Feuillet and Eversole 2007) have been conducted by the IWGSC and other research institutions since 2005. Physical maps (Korol et al. 2009; Fleury et al. 2010;

Luo et al. 2010) 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 Mb) 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, polyploid genomes using a chromosome-based approach. These efforts develop the needed background and tools for sequencing the hexaploid and diploid wheat genomes and provide theoretical evolutionary perspectives and excellent tools for unfolding 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 crop improvement, both qualitatively and quantitatively. Upon completion of genome sequencing of either diploid wild wheat, *T. urartu* or *Ae. tauschii*, or hexaploid bread wheat, domestication syndrome factors and other relevant genes and QTL could be isolated, and effects of wheat domestication could be accurately estimated. The improvement of bread wheat is a future challenge for mankind, based on the evidence and ideas presented above and presented much earlier by Aaronsohn (Aaronsohn and Schweinfurth 1906; Aaronsohn 1910), and based on the distinct adaptive complexes of *T. dicoccoides* to environmental stress and their direct relevance to wheat domestication (Nevo et al. 2002).

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References

Aaronsohn A (1910) Agricultural and botanical explorations in Palestine. Bureau of Plant Industry Bull 80, USDA, No 180

Aaronsohn A, Schweinfurth G (1906) Die Auffindung des wilden Emmers (*Triticum dicoccum*) in Nordpalästina. Altneuland Monatsschrift für die irtschaft. Erschliessung Palästinas 7–8:213–220

Akhunov ED, Akhunova AR, Anderson OD, Anderson JA, Blake N, Clegg MT, Coleman-Derr D, Conley EJ, Crossman CC, Deal KR, Dubcovsky J, Gill BS, Gu YQ, Hadam J, Heo H, Huo N, Lazo GR, Luo MC, Ma YQ, Matthews DE, McGuire PE, Morrell PL, Qualset CO, Renfro J, Tabanao D, Talbert LE, Tian C, Toleno DM, Warburton ML, You FM, Zhang W, Dvorak J (2010) Nucleotide diversity maps reveal variation in diversity among wheat genomes and chromosomes. BMC Genomics 11:702

Allaby RG (2010) Integrating the processes in the evolutionary system of domestication. J Exp Bot 61:935–944

Araki E, Miura H, Sawada S (1999) Identification of genetic loci affecting amylose content and agronomic traits on chromosome 4A of wheat. Theor Appl Genet 98:977–984

Balter M (2007) Seeking agriculture's ancient roots. Science 316:1830–1835

Belyayev A, Kalendar R, Brodsky L, Nevo E, Schulman AH, Raskina O (2010) Transposable elements in a marginal plant population: temporal fluctuations provide new insights into genome evolution of wild diploid wheat. Mobile DNA 1:6

Bennett MD, Leitch IJ (2010) Plant DNA *C*-values database (release 5.0, Dec. 2010). http://www.kew.org/cvalues/

Börner A, Korzun V, Worland AJ (1998) Comparative genetic mapping of loci affecting plant height and development in cereals. Euphytica 100:245–248

Brown AHD (2010) Variation under domestication in plants: 1859 and today. Phil Trans R Soc B 365:2523–2530

Buckler ES, Thornsberry JM, Kresovich S (2001) Molecular diversity, structure and domestication of grasses. Genet Res 77:213–218

Cakmak IA, Torun E, Millet E, Feldman M, Fahima T, Korol AB, Nervo E, Braun HJ, Özkan H (2004) *Triticum dicoccoides*: an important genetic resource for increasing zinc and iron concentration in modern cultivated wheat. Soil Sci Plant Nutr 50:1047–1054

Campbell B, Baenziger PS, Gill KS, Eskridge KM, Budak H, Erayman M, Dweikat I, Yen Y (2003) Identification of QTLs and environmental interactions associated with agronomic traits on chromosome 3A of wheat. Crop Sci 43:1493–1505

Cao W, Scoles GJ, Hucl P (1997) The genetics of rachis fragility and glume tenacity in semi-wild wheat. Euphytica 94:119–124

Carver BF (2009) Wheat science and trade. Wiley, Danvers, p 569

Chao S, Dubcovsky J, Dvorak J, Luo MC, Baenziger SP, Matnyazov R, Clark DR, Talbert LE, Anderson JA, Dreisigacker S, Glover K, Chen J, Campbell K, Bruckner PL, Rudd JC, Haley SD, Carver BF, Perry S, Sorrells ME, Akhunov ED (2010) Population- and genome-specific patterns of linkage disequilibrium and SNP variation in spring and winter wheat (*Triticum aestivum* L.). BMC Genomics 11:727

Chen QF, Yen C, Yang JL (1998) Chromosome location of the gene for brittle rachis in the Tibetan weedrace of common wheat. Genet Res Crop Evol 45:21–25

Cockram J, Jones H, Leigh FJ, O'Sullivan D, Powell W, Laurie DA, Greenland AJ (2007) Control of flowering time in temperate cereals: genes, domestication, and sustainable productivity. J Exper Bot 58:1231–1244

Cockram J, Norris C, O'Sullivan DM (2009) PCR-based markers diagnostic for Spring and Winter seasonal growth habit in barley. Crop Sci 49:403–410

Damania AB (1998) Diversity of major cultivated plants domesticated in the Near East. In: Damania AB, Valkoun J, Willcox G, Qualset CO (eds) The origins of agriculture and crop domestication. Proceedings of the Harlan Symposium. ICARDA, Aleppo, pp 51–64

Darwin C (1905) The variation of animals and plants under domestication. John Murray, London (popular edition in two volumes) 566 p

Doebley J (1989) Isozymic evidence and the evolution of crop plants. In: Soltis D, Soltis P (eds) Isozymes in Plant Biology. Dioscorides Press, Portland, pp 165–191

Doebley JF, Gaut BS, Smith BD (2006) The molecular genetics of crop domestication. Cell 127:1309–1321

Dorofeev VF, Filatenko AA, Migushova EF, Udaczin RA, Jakubziner MM (1979) Wheat. In: Dorofeev VF, Korovina ON (eds) Flora of Cultivated Plants, vol 1. Leningrad, Russia

Dubcovsky J, Dvorak J (2007) Genome plasticity a key factor in the success of polyploid wheat under domestication. Science 316:1862–1866

Dunford RP, Griffiths S, Christodoulou V, Laurie DA (2005) Characterisation of a barley (*Hordeum vulgare* L.) homologue of the Arabidopsis flowering time regulator GIGANTEA. Theor Appl Genet 110:925–931

Dvorak J (2009) Triticeae genome structure and evolution. In: Feuiller C, Muehlbauer GJ (eds) Genetics and genomics of the Triticeae, plant genetics and genomics: crops and models 7. Springer, Berlin, pp 685–711

Dvorak J, Akhunov E (2005) Tempos of gene locus deletions and duplications and their relationship to recombination rate during diploid and polyploid evolution in the *Aegilops-Triticum* alliance. Genetics 17:323–332

Dvorak J, Diterlizzi P, Zhang HB, Resta P (1993) The evolution of polyploidy wheats: identification of the A genome donor species. Genome 36:21–31

Dvorak J, Luo MC, Yang ZL (1998) Genetic evidence on the origin of *Triticum aestivum* L. In: Damania AB, Valkoun J, Willcox G, Qualset CO (eds) The origins of agriculture and crop domestication. Proceedings of the Harlan symposium. ICARDA, Aleppo, pp 235–251

Dvorak J, Akhunov ED, Akhunov AR, Deal KR, Luo MC (2006) Molecular characterization of a diagnostic DNA marker for domesticated tetraploid wheat provides evidence for gene flow from wild tetraploid wheat to hexaploid wheat. Mol Biol Evol 23:1386–1396

Dvorak J, Luo MC, Akhunov ED (2011) N.I. Vavilov's theory of centers of diversity in light of current understanding of wheat diversity, domestication and evolution. Czech J Genet Plant Breed (in press)

Elias EM, Steiger KD, Cantrell RG (1996) Evaluation of lines derived from wild emmer chromosome substitutions II. Agronomic traits. Crop Sci 36:228–233

Faris J, Gill BS (2002) Genomic targeting and high resolution mapping of the domestication gene *Q* in wheat. Genome 45:706–718

Faris JD, Fellers JP, Brooks SA, Gill BS (2003) A bacterial artificial chromosome contig spanning the major domestication locus *Q* in wheat and identification of a candidate gene. Genetics 164:311–321

Faris JD, Simons KJ, Zhang Z, Gill B (2005) The wheat super domestication gene *Q*. Front Wheat Biosci 100:129–148

Faure S, Higgins J, Turner A, Laurie DA (2007) The FLOWERING LOCUS T-like gene family in barley (*Hordeum vulgare*). Genetics 176:599–609

Feldman M, Kislev ME (2007) Domestication of emmer wheat and evolution of free-threshing tetraploid wheat. Israel J Plant Sci 55:207–221

Feldman M, Sears ER (1981) The wild gene resources of wheat. Sci Am 244:102–112

Feldman M, Lupton FGH, Miller TE (1995) Wheats. *Triticum* spp. (Gramineae- Triticinae). In: Smartt J, Simmonds NW (eds) Evolution of crop plants. Longman Scientific & Technical Press, London, pp 84–192

Feuillet C, Eversole K (2007) Physical mapping of the wheat genome: a coordinated effort to lay the foundation for genome sequencing and develop tools for breeders. Isr J Plant Sci 55:307–313

Feuillet C, Muehlbauer GJ (2009) Genetics and genomics of the Triticeae, plant genetics and genomics: crops and models 7. Springer, Berlin

Fleury D, Luo MC, Dvorak J, Ramsay L, Gill BS, Anderson OD, You FM, Shoaei Z, Deal KR, Langridge P (2010) Physical mapping of a large plant genome using global high-information-content-fingerprinting: the distal region of the wheat ancestor *Aegilops tauschii* chromosome 3DS. BMC Genomics 11:382

Frary A, Doğanlar S (2003) Comparative genetics of crop plant domestication and evolution. Turk J Agric Forest 27:59–69

Fu YB, Somers DJ (2009) Genome-wide reduction of genetic diversity in wheat breeding. Crop Sci 49:61–168

Fuller DQ (2007) Contrasting patterns in crop domestication and domestication rates: recent archaeobotanical insights from the Old World. Ann Bot 100:903–924

Fuller DQ, Allaby RG, Stevens C (2010) Domestication as innovation: the entanglement of techniques, technology and chance in the domestication of cereal crops. World Archaeol 42:13–28

Gandilian PA (1972) On wild growing *Triticum* species of Armenian SSR. Bot Zhur 57:173–181

Gegas VC, Nazari A, Griffiths S, Simmonds J, Fish L, Orford S, Sayers L, Doonan JH, Snape JW (2010) A genetic framework for grain size and shape variation in wheat. Plant Cell 22:1046–1056

Gepts P (2004) Crop domestication as a long-term selection experiment. Plant Breed Rev 24:1–44

Giles RJ, Brown TA (2006) *GluDy* allele variations in *Aegilops tauschii* and *Triticum aestivum*: implications for the origins of hexaploid wheats. Theor Appl Genet 112: 1563–1572

Gill KS, Gill BS, Endo TR, Boyko EV (1996a) Identification and high-density mapping of gene-rich regions in chromo some group 5 of wheat. Genetics 143:1001–1012

Gill KS, Gill BS, Endo TR, Taylor T (1996b) Identification and high-density mapping of gene-rich regions in chromosome 1 of wheat. Genetics 144:1883–1891

Gill BS, Friebe B, Raupp WJ, Wilson DL, Cox TS, Sears RG, Brown-Guedira GL, Fritz AK (2006) Wheat genetics resource center: the first 25 years. Adv Agron 89:73–136

Gill BS, Li W, Sood S, Kuraparthy V, Friebe Simons KJ, Zhang Z, Faris JD (2007) Genetics and genomics of wheat domestication-driven evolution. Isr J Plant Sci 55: 223–229

Griffiths S, Dunford RP, Coupland G, Laurie DA (2003) The evolution of CONSTANS-like gene families in barley, rice and Arabidopsis. Plant Physiol 131:1855–1867

Gupta PK, Mir RR, Mohan A, Kumar J (2008) Wheat genomics: present status and future prospects. Intl J Plant Genomics, vol 2008, Article ID 896451, 36 pages. doi: 10.1155/2008/896451

Gustafson P, Raskina O, Ma X, Nevo E (2009) Wheat evolution, domestication, and improvement. In: Carver BF (ed) Wheat: science and trade. Wiley, Danvers, pp 5–30

Hancock JF (2005) Contributions of domesticated plant studies to our understanding of plant evolution. Ann Bot 96: 953–963

Harlan JR (1992) Crop and man. American Society of Agronomy, Crop Science Society of America, Madison

Haudry A, Cenci A, Ravel C, Bataillon T, Brunel D, Poncet C, Hochu I, Poirier S, Santoni S, Gle′min S, David J (2007) Grinding up wheat: a massive loss of nucleotide diversity since domestication. Mol Biol Evol 24:1506–1517

Hedden P (2003) The genes of the green revolution. Trends Genet 19:5–9

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

Hillman G, Davies S (1990) Measured domestication rates in wild wheats and barley under primitive cultivation, and their archaeological implications. J World Prehistory 4:157–222

Honne BI, Heun M (2009) On the domestication genetics of self-fertilizing plants. Veget Hist Archaeobot 18:269–272

Huang S, Sirikhachornkit A, Su X, Faris J, Gill B, Haselkorn R, Gornicki P (2002) Genes encoding plastid acetyl-CoA carboxylase and 3-phosphoglycerate kinase of the *Triticum/Aegilops* complex and the evolutionary history of polypoid wheat. Proc Natl Acad Sci USA 99:8133–8138

Inda LA, Segarra-Moragues José Gabriel, Müller Jochen, Peterson Paul M, Catalán Pilar (2008) Dated historical biogeography of the temperate LoHinae (Poaceae, Pooideae) grasses in the northern and southern hemispheres. Mol Phylogenet Evol 46:932–957

Jantasuriyarat C, Vales MI, Watson CJW, Riera-Lizarazu O (2004) Identification and mapping of genetic loci affecting the free-threshing habit and spike compactness in wheat (*Triticum aestivum* L.). Theor Appl Genet 108: 261–273

Johnson BL (1975) Identification of the apparent B-genome donor of wheat. Can J Genet Cytol 17:21–39

Johnson RC (2008) Gene banks pay big dividends to agriculture, the environment, and human welfare. PLoS Biol 6(6):e148. doi:10.1371/journal.pbio.0060148

Johnson BL, Dhaliwal HS (1976) Reproductive isolation of *Triticum boeticum* and *Triticum urartu* and the origin of the tetraploid wheats. Am J Bot 63:1088–1094

Kashkush K (2007) Genome-wide impact of transcriptional activation of long terminal repeat retrotransposons on the expression of adjacent host genes. Isr J Plant Sci 55: 241–250

Kashkush K, Feldman M, Levy AA (2002) Gene loss, silencing and activation in a newly synthesized wheat allotetraploid. Genetics 160:1651–1656

Kato K, Miura H, Akiyama M, Kuroshima M, Sawada S (1998) RFLP mapping of the three major genes, *Vrn1*, *Q* and *B1*, on the long arm of chromosome 5A of wheat. Euphytica 101:91–95

Kato K, Miura H, Sawada S (2000) Mapping QTLs controlling grain yield and its components on chromosome 5A of wheat. Theor Appl Genet 101:933–943

Kato K, Sonokawa R, Miura H, Sawada S (2003) Dwarfing effect associated with the threshability gene *Q* on wheat chromosome 5A. Plant Breed 122:489–492

Kellogg EA (2001) Evolutionary history of the grasses. Plant Physiol 125:1198–1205

Kerber ER (1964) Wheat: reconstitution of the tetraploid component (AABB) of hexaploids. Science 143: 253–255

Kerber RE, Rowland GG (1974) Origin of the threshing character in hexaploid wheat. Can J Genet Cytol 16: 145–154

Kihara H (1944) Discovery of the DD-analyser, one of the ancestors of *Triticum vulgare*. Agric Hortic (Tokyo) 19: 13–14

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

Kilian B, Özkan H, Pozzi C, Salamini F (2009) Domestication of the Triticeae in the Fertile Crescent. In: Feuillet C, Muehlbauer GJ (eds) Genetics and genomics of the Triticeae, plant genetics and genomics: crops and models 7. Springer, Berlin, pp 81–119

Kislev ME (1980) *Triticum parvicoccum* sp. *nov*., the oldest naked wheat. Israel J Bot 28:95–107

Kislev ME, Nadel D, Carmi I (1992) Epipalaeolithic (19,000 BP) cereal and fruit diet at Ohalo II, Sea of Galilee, Israel. Rev Palaeobot Palynol 73:161–166

Konishi S, Izawa T, Lin SY, Ebana K, Fukuta Y, Sasaki T, Yano M (2006) An SNP caused loss of seed shattering during rice domestication. Science 312:1392–1396

Korol A, Mester D, Frenkel Z, Ronin Y (2009) Methods of genetic analysis in the Triticeae. In: Feuillett C, Muelbauer GJ (eds) Genetics and genomics of the Triticeae, plant genetics and genomics: crops and models 7. Springer, Berlin, pp 163–199

Kuckuck H (1959) Neuere Arbeiten zur Entstehung der hexaploiden Kulturweizen. Z. Pflanzenzüchtg. 41:205–226

Kunzel G, Korzum L, Meister A (2000) Cytologically integrated physical restriction fragment length polymorphism maps for the barley genome based on translocation breakpoints. Genetics 154:397–412

Kuraparthy V, Sood S, Chunneja P, Dhaliwal HS, Gill BS (2007) Identification and mapping of tiller inhibition gene (*tin3*) in wheat. Theor Appl Genet 114:285–294

Kuraparthy V, Sood S, Gill BS (2008) Genomic targeting and mapping of tiller inhibition gene (*tin3*) of wheat using ESTs and synteny with rice. Funct Integr Genomics 8:33–42

Levy AA, Feldman M (2004) Genetic and epigenetic reprogramming of the wheat genome upon allopolyploidization. Biol J Linn Soc 82:607–613

Li W, Gill BS (2006) Multiple genetic pathways for seed shattering in the grasses. Func Integr Genomics 6: 300–309

Li YC, Fahima T, Korol AB, Peng J, Röder MS, Kirzhner VM, Beiles A, Nevo E (2000) Microsatellite diversity correlated with ecological-edaphic and genetic factors in three microsites of wild emmer wheat in North Israel. Mol Biol Evol 17:851–862

Li YC, Korol AB, Fahima T, Beiles A, Nevo E (2002) Microsatellites: genomic distribution, putative functions and mutational mechanisms: a review. Mol Ecol 11: 2453–2465

Li YC, Fahima T, Röder MS, Kirzhner VM, Beiles A, Korol AB, Nevo E (2003) Genetic effects on microsatellite diversity in wild emmer wheat (*Triticum dicoccoides*) at the Yehudiyya microsite, Israel. Heredity 90:156–160

Li YC, Korol AB, Fahima T, Nevo E (2004) Microsatellites within genes: structure, function and evolution. Mol Biol Evol 21:991–1007

Liu YG, Tsunewaki K (1991) Restriction fragment length polymorphism analysis of wheat. II. Linkage maps of the RFLP sites in common wheat. Jpn J Genet 66:617–633

Luo MC, Yang ZL, Dvorak J (2000) The *Q* locus of Iranian and European spelt wheat. Theor Appl Genet 100:602–606

Luo MC, Yang ZL, You FM, Kawahara T, Waines JG, Dvorak J (2007) The structure of wild and domesticated emmer wheat populations, gene flow between them, and the site of emmer domestication. Theor Appl Genet 114:947–959

Luo MC, Deal KR, Akhunov ED, Akhunova AR, Anderson OD, Anderson JA, Blake N, Clegg MT, Coleman-Derr D, Conley EJ, Crossman CC, Dubcovsky J, Gill BS, Gu YQ, Hadam J, Heo HY, Huo N, Lazo G, Ma Y, Matthews DE, McGuire PE, Morrell PL, Qualset CO, Renfro J, Tabanao D, Talbert LE, Tian C, Toleno DM, Warburton ML, You FM, Zhang W, Dvorak J (2009) Genome comparisons reveal a dominant mechanism of chromosome number reduction in grasses and accelerated genome evolution in Triticeae. Proc Natl Acad Sci USA 106:15780–15785

Luo MC, Ma Y, You FM, Anderson OD, Kopecký D, Šimková H, Šafář J, Doležel J, Gill BS, McGuire PE, Dvorak J (2010) Feasibility of physical map construction from fingerprinted bacterial artificial chromosome libraries of polyploid plant species. BMC Genomics 11:122

Matsuoka Y, Nasuda S (2004) Durum wheat as a candidate for the unknown female progenitor of bread wheat: an empirical study with a highly fertile F_1 hybrid with *Aegilops tauschii* Coss. Theor Appl Genet 109:1710–1717

McFadden ES, Sears ER (1946) The origin of *Triticum spelta* and its free-threshing hexaploid relatives. J Hered 37(81–89):107–116

McKey J (1966) Species relationships in *Triticum*. Hereditas 2:237–276

Mori N, Ishii T, Ishido T, Hirosawa S, Watatani H, Kawahara T, Nesbitt M, Belay G, Takumi S, Ogihara Y, Nakamura C (2003) Origin of domesticated emmer and common wheat inferred from chloroplast DNA fingerprinting. 10th international wheat genetics symposium. Paestum, pp 25–28

Muramatsu M (1963) Dosage effect of the spelta gene *q* of hexaploid wheat. Genetics 48:469–482

Nalam V, Vales MI, Watson CJW, Kianian SF, Riera-Lizarazu O (2006) Map based analysis of genes affecting the brittle rachis character in tetraploid wheat (*Triticum turgidum*). Theor Appl Genet 112:373–381

Nalam V, Vales MI, Watson CJW, Johnson EB, Riera-Lizarazu O (2007) Map based analysis of genetic loci on chromosome 2D that affect glume tenacity and threshability, components of the free-threshing habit in common wheat (*Triticum aestivum* L.). Theor Appl Genet 116:135–145

Nesbitt M, Samuel D (1996) From stable crop to extinction? The archaeology and history of the hulled wheats. In: Padulosi S, Hammer K, Heller J (eds) hulled wheats. International Plant Genetic Resources Institute, Rome, pp 41–100

Nevo E (2004) Genomic diversity in nature and domestication. In: Henry R (ed) Diversity and evolution of plants. Genotypic and phenotypic variation in higher plants. CABI Publishing CAB International, Wallingford, pp 287–315

Nevo E (2007) Evolution of wild wheat and barley and crop improvement: studies at the Institute of Evolution. Isr J Plant Sci 55:251–263

Nevo E (2009) Ecological genomics of natural plant populations: the Israeli perspective. In: Somers DJ, Langridge P, Gustafson JP (eds) Methods in molecular biology, plant genomics, vol 513. Human Press, A part of Springer Science + Business Media, pp 321–344

Nevo E (2011) Triticum. In: Kole C (ed) Wild crop relatives: genomic and breeding resources, cereals. Springer, Berlin, pp 407–456. doi:10.1007/978-3-642-14228-4_10

Nevo E, Beiles A (1989) Genetic diversity of wild emmer wheat in Israel and Turkey: structure, evolution and application in breeding. Theor Appl Genet 77:421–455

Nevo E, Chen G (2010) Drought and salt tolerances in wild relatives for wheat and barley improvement. Plant Cell Environment 33:670–685. doi:10.1111/j.1365-3040.2009.02107.x

Nevo E, Korol AB, Beiles A, Fahima T (2002) Evolution of Wild Emmer and Wheat Improvement: Population Genetics, Genetic Resources, and Genome Organization of Wheat's Progenitor, *Triticum dicoccoides*. Springer, Berlin 364

Otto SP, Barton NH (1997) The evolution of recombination: removing the limits to natural selection. Genetics 147: 879–906

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

Özkan H, Brandolini A, Pozzi C, Effgen S, Wunder J, Salamini F (2005) A reconsideration of the domestication geography of tetraploid wheats. Theor Appl Genet 110:1052–1060

Özkan H, Willcox G, Graner A, Salamini F, Kilian B (2010) Geographic distribution and domestication of wild emmer wheat (*Triticum dicoccoides*). Genet Resour Crop Evol 58:11–53. doi:10.1007/s10722-010-9581-5

Parsons P (2005) Environments and evolution: interactions between stress, resource inadequacy and energetic efficiency. Biol Rev 80:589–610

Paterson AH, Lin YR, Li Z, Schertz KF, Doebley JF, Pinson SRM, Liu SC, Stansel JW, Irvine JE (1995) Convergent domestication of cereal crops by independent mutations at corresponding genetic loci. Science 269:1714–1718

Paux E, Sourdille P (2009) A toolbox for Triticeae genomics. In: Feuillet C, Muehlbauer GJ (eds) Genetics and genomics of the Triticeae, plant genetics and genomics: crops and models 7. Springer, Berlin, pp 255–283

Paux E, Sourdille P, Salse J, Saintenac C, Choulet F, Leroy P, Korol A, Michalak M, Kianian S, Spielmeyer W, Lagudah E, Somers D, Kilian A, Alaux M, Vautrin S, Bergès H, Eversole K, Appels R, Safar J, Simkova H, Dolezel J, Bernard M, Feuillet C (2008) Physical map of the 1-Gigabase bread wheat chromosome 3B. Science 322: 101–104

Peng JH, Korol AB, Fahima T, Röder MS, Ronin YI, Li YC, Nevo E (2000) Molecular genetic maps in wild emmer wheat, *Triticum dicoccoides*: genome-wide coverage, massive negative interference, and putative quasi-linkage. Genome Res 10:1509–1531

Peng JH, Ronin Y, Fahima T, Röder MS, Li YC, Nevo E, Korol A (2003) Domestication quantitative trait loci in *Triticum dicoccoides*, the progenitor of wheat. Proc Natl Acad Sci USA 100:2489–2494

Peng JH, Zadeh H, Lazo GR, Gustafson JP, Chao S et al (2004) Chromosome bin map of expressed sequence tags in homoeologous group 1 of hexaploid wheat and homoeology with rice and Arabidopsis. Genetics 168:609–623

Perrino P, Laghetti G, D'Antuono LF, Al Ajlouni M, Kanbertay M, Szabo AT, Hammer K (1996) Ecogeographical distribution of hulled wheat species. In: Padulosi S, Hammer K, Heller J (eds) Hulled wheats. International Plant Genetic Resources Institute, Rome, pp 102–118

Piperno DR, Weiss E, Holst I, Nadel D (2004) Processing of wild cereal grains in the Upper Palaeolithic revealed by starch grain analysis. Nature 430:670–673

Rice WR (2002) Experimental tests of the adaptive significance of sexual recombination. Nat Rev Genet 3:241–251

Röder MS, Korzun V, Wendehake K, Plaschke J, Tixier MH et al (1998) A microsatellite map of wheat. Genetics 149:2007–2023

Rong J, Millet E, Manisterski J, Feldman M (2000) A new powdery mildew resistance gene: introgression from wild emmer into common wheat and RFLP-based mapping. Euphytica 115:121–126

Ross-Ibarra J, Morrell PL, Gaut BS (2007) Plant domestication, a unique opportunity to identify the genetic basis of adaptation. Proc Natl Acad Sci USA 104:8641–8648

Rossini L, Vecchietti A, Nicoloso, Stein N, Franzago S, Salamini F, Pozzi C (2006) Candidate genes for barley mutants involved in plant architecture: an *in silico* approach. Theor Appl Genet 112:1073–1085

Sabot F, Schulman AH (2009) Genomics of transposable elements in the Triticeae. In: Feuillett C, Muelbauer GJ (eds) Genetics and genomics of the triticeae, plant genetics and genomics: crops and models 7. Springer, Berlin, pp 387–405

Salamini F, Özkan H, Brandolini A, Schäfer-Pregl R, Martin W (2002) Genetics and geography of wild cereal domestication in the Near East. Nat Rev Genet 3:429–441

Schuster SC (2008) Next-generation sequencing transforms today's biology. Nat Methods 5:16–18

Sears ER (1954) The aneuploids of common wheat. Res Bull Missouri Agric Exp Stn 572:1–57

Shah M, Gill KS, Bezinger PS, Yen Y, Kaeppler SM, Ariyarathne HM (1999) Molecular mapping of loci for agronomic traits on chromosome 3A of bread wheat. Crop Sci 39:1728–1732

Sharma H, Waynes J (1980) Inheritance of tough rachis in crosses of *Triticum monococcum* and *Triticum boeoticum*. J Hered 7:214–216

Simons K, Fellers JP, Trik HN, Zhang Z, Tai YS, Gill BS, Faris JD (2006) Molecular characterization of the major wheat domestication gene *Q*. Genetics 172:547–555

Snape J, Law W, Parker CN, Worland BB, Worland AJ (1985) Genetical analysis of chromosome 5A of wheat and its influence on important agronomic characters. Theor Appl Genet 71:518–526

Sood S, Kuraparthy V, Bai G, Gill BS (2009) The major threshability genes soft glume (*sog*) and tenacious glume (*Tg*), of diploid and polyploid wheat, trace their origin to independent mutations at non-orthologous loci. Theor Appl Genet 119:341–351

Spielmeyer W, Richards RA (2004) Comparative mapping of wheat chromosome 1AS which contains the tiller inhibition gene (*tin*) with rice chromosome 5S. Theor Appl Genet 109:1303–1310

Stein N (2009) Physical mapping in the Triticeae. In: Feuillet C, Muehlbauer GJ (eds) Genetics and genomics of the Triticeae, plant genetics and genomics: crops and models 7. Springer, Berlin, pp 317–335

Tanksley SD, McCouch SR (1997) Seed banks and molecular maps: unlocking genetic potential from the wild. Science 277:1063–1066

Tanno K, Willcox G (2006) How fast was wild wheat domesticated? Science 311:1886

Thuillet AC, Bataillon T, Poirier S, Santoni S, David JL (2005) Estimation of long-term effective population sizes through the history of Durum wheat using microsatellite data. Genetics 169:1589–1599

Turner A, Beales J, Faure S, Dunford RP, Laurie DA (2005) The pseudo-response regulator Ppd-H1 provides adaptation to photoperiod in barley. Science 310:1031–1034

Uauy C, Distelfield A, Fahima T, Blechl A, Dubcovsky J (2006) A NAC gene regulating senescence improves grain protein, zinc and iron content in wheat. Science 413: 1298–1301

van Zeist W, Bakker-Heeres JAH (1985) Archaeological studies in the Levant 1. Neolithic sites in the Damascus Basin: Aswad, Ghoraife, Ramad. Palaeohistoria 24: 165–256

Villareal R, Mujeeb-Kazi A, Rajaram S (1996) Inherintance of threshability in synthetic hexaploid by *T. aestivum* crosses. Plant Breed 115:407–409

Watanabe N (2005) The occurrence and inheritance of a brittle rachis phenotype in Italian durum wheat cultivars. Euphytica 142:247–251

Watanabe N, Ikebata N (2000) The effects of homoeologous group 3 chromosomes on grain colour dependent seed dormancy and brittle rachis in tetraploid wheat. Euphytica 115:215–220

Watanabe N, Sogiyama K, Yamagashi Y, Skata Y (2002) Comparative telosomic mapping of homoeologous genes for brittle rachis in tetraploid and hexaploid wheats. Hereditas 137:180–185

Willcox G (2004) Measuring grain size and identifying Near Eastern cereal domestication: evidence from the Euphrates valley. J Archaeol Sci 31:145–150

Willcox G, Fornite S, Herveaux L (2008) Early Holocene cultivation before domestication in Northern Syria. Veget Hist Archaeobot 17:313–325

Xie W, Nevo E (2008) Wild emmer: genetic resources, gene mapping and potential for wheat improvement. Euphytica 164:603–614

Yan L, Loukoianov A, Tranquilli G, Helguera M, Fahima T, Dubcovsky J (2003) Positional cloning of the wheat vernalization gene *VRN1*. Proc Natl Acad Sci USA 100:6263–6268

Zohary D, Hopf M (2000) Domestication of plants in the old world. Oxford University Press, Oxford