Evolution of Polyploid *Triticum* Wheats under Cultivation: The Role of Domestication, Natural Hybridization and Allopolyploid Speciation in their Diversification

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The evolution of the polyploid *Triticum* wheats is distinctive in that domestication, natural hybridization and allopolyploid speciation have all had significant impacts on their diversification. In this review, I outline the phylogenetic relationships of cultivated wheats and their wild relatives and provide an overview of the recent progress and remaining issues in understanding the genetic and ecological factors that favored their evolution. An attempt is made to view the evolution of the polyploid *Triticum* wheats as a continuous process of diversification that was initiated by domestication of tetraploid emmer wheat and driven by various natural events ranging from interploidy introgression via hybridization to allopolyploid speciation of hexaploid common wheat, instead of viewing it as a group of discrete evolutionary processes that separately proceeded at the tetraploid and hexaploid levels. This standpoint underscores the important role of natural hybridization in the reticulate diversification of the tetraploid–hexaploid *Triticum* wheat complex and highlights critical, but underappreciated, issues that concern the allopolyploid speciation of common wheat.

**Keywords:** *Aegilops* • Hybrid swarms • Interploidy introgression • Non-reductional meiosis • *Triticum* • Unreduced gamete formation.

**Abbreviations:** AFLPs, amplified fragment length polymorphisms; cpDNA, chloroplast DNA; RFLPs, for restriction fragment length polymorphisms.

**Introduction**

Agriculture began in the Neolithic period ~10,000 years before present (Smith 1998). Since the beginnings of agriculture, agroecosystems (i.e. ecosystems impacted by the practice of agriculture) have expanded around the globe and now cover ~38% of the earth’s landmass, excluding Antarctica (FAO 2009). In these geologically new environments, a group of plants that have symbiotic association with humans evolved from wild plants through domestication in both the Old and New Worlds. Subsequently, some of those plants became staple-food crops on which large proportions of the world’s populations rely for daily sustenance. In today’s high-population-growth world, crops have evident agronomic and economic value as important resources for food, clothing, fodder, medicine and many other products.

As Darwin (1859) pointed out, crops provide a fascinating source of materials for evolutionary biologists, because crop domestication and diversification can serve as usable genetic and ecological models to study human–plant interactions. The morphological and physiological properties of crops that are absent in their wild ancestors are indicative of the fine adaptations that have occurred in agroecological environments. Domestication and race diversification are complex evolutionary processes in which the genetic forces of mutation, selection and genetic drift have significant roles. How these forces shaped the crop genomes and what genetic changes are responsible for the crops’ adaptive transformations can be studied in depth using their wild ancestors as the living references. Such studies may deepen our understanding of the genetic mechanisms of adaptations in nature, because the interplay of those genetic forces is also important in the process of population divergence and speciation that occur in natural environments.

Modern molecular biology studies have provided insights into the genetic underpinning of selection during plant domestication and diversification. As a consequence, a better understanding has been achieved of the origins of major cereal crops, such as rice, barley and maize, that were domesticated from their wild ancestors without undergoing changes in ploidy (Doebley et al. 2006). In contrast, much remains to be learned about the origins and evolution of other crops. Cultivated tetraploid and hexaploid *Triticum* wheats, such as domesticated emmer wheat, durum wheat and common wheat, provide examples of those crops that require novel approaches to study the modes of their domestication and diversification. The picture of polyploid wheat evolution under cultivation is distinctive in that natural hybridization and allopolyploid speciation had a significant role in its diversification.
In this review, I begin with an outline of the phylogenetic relationships of cultivated wheats and their wild relatives, and then provide an overview of the recent progress and remaining issues in understanding the genetic and ecological factors that favored their evolution. An attempt is made here to view the evolution of the polyploid *Triticum* wheats under cultivation as a continuous process of diversification that embraces the tetraploid and hexaploid levels. The goal of this review is to underscore the significant role of natural hybridization in the diversification of polyploid *Triticum* wheats and highlight the previously underappreciated questions that concern allopolyploid speciation of hexaploid wheats.

**Phylogeny of cultivated wheats**

Cultivated wheats and their close wild relatives belong to the genus *Triticum* L., a member of the tribe Triticeae, which contains ~300 species (Clayton and Renvoize 1986). Barley (*Hordeum vulgare* L. subsp. *vulgare*) is another economically important cereal crop of the tribe Triticeae. The wheat genus *Triticum* has a relatively small number of species (six species) with wild taxa occurring in the Middle East and Transcaucasus region. This is in good contrast to the case of the barley genus *Hordeum*, which consists of 31 species that naturally grow in temperate and dry regions of western and eastern Eurasia, North and South America and South Africa (Blattner 2006). The homeland of *Triticum* and *Hordeum* is in southwest Asia and the divergence time of the wheat and barley lineages is estimated to be ~13 million years ago (middle Miocene) (Gaut 2002).

The genus *Triticum* consists of six species: *Triticum monococcum* L. (AA genome); *Triticum urartu* Tumanian ex Gandilyan (AA genome); *Triticum turgidum* L. (AABB genome); *Triticum timopheevii* (Zhuk.) Zhuk. (AAGG genome); *Triticum aestivum* L. (AABBDD genome); and *Triticum zhukovskyi* Menabde & Eriz. (AAAAGG genome). These species are grouped into three sections: Sect. Monococcon (consisting of diploid species); Sect. Dicoccoidea (consisting of tetraploid species); and Sect. Triticum (consisting of hexaploid species). Of these species, *T. urartu* exists only in its wild form, whereas *T. aestivum* and *T. zhukovskyi* exist only as cultivated forms. The other species, *T. monococcum*, *T. turgidum* and *T. timopheevii*, have both a wild and a domesticated form. All *Triticum* species are native to the ‘Fertile Crescent’ of the Near East, which encompasses the eastern Mediterranean, southeastern Turkey, northern Iraq and western Iran, and its neighboring regions of the Transcausus, and northern Iran (Fig. 1). Many of the cultivated wheats and their close wild relatives are referred to by common names (Table 1).

Allopolyploidization via hybridization with a species of the genus *Aegilops* was the major force leading to diversification during the evolution of *Triticum* species (Tsunewaki 2009) (Fig. 2). The diploid AA genome species, *T. monococcum* and *T. urartu*, diverged less than one million years ago (Huang et al. 2002). Evidence based on morphological, cytological and genetic studies suggests that, after the divergence of *T. monococcum* and *T. urartu*, the tetraploid AABB and AAGG genome species evolved less than 0.5 million years ago through hybridization between *T. urartu* and a species that belonged to the lineage of the current wild wheat species, *Aegilops speltoides* Tausch (SS genome). In this process, at least two independent hybridization events are believed to have occurred: one associated with the origin of *T. turgidum* (AABB genome), and the other with the origin of *T. timopheevii* (AAGG genome) (Sarkar and Stebbins 1956, Shands and Kimber 1973, Chapman et al. 1976, Dvorak 1976, Dvorak et al. 1988, 1993, Ogihara and Tsunewaki 1988, Noda and Ge 1989, Dvorak and Zhang 1990, Miyashita et al. 1994, Huang et al. 2002, Kilian et al. 2007a).

The genesis of the AABB and AAGG genome tetraploid species set the stage for further diversification through allopolyploid speciation some hundreds of thousands of years later (Fig. 2). During the development of agriculture in the Fertile Crescent ~10,000 years ago, *T. turgidum* and *T. timopheevii* were domesticated and their cultivated forms appeared (Feldman 2001, Salamin et al. 2002). The diploid *T. monococcum* also was domesticated in the same area (for the process of einkorn domestication, see Tanno and Willox 2006, Kilian et al. 2007b). After this period, the hexaploid *Triticum* wheats emerged through natural hybridization between the tetraploid cultivars and diploid *Aegilops* and *Triticum* species. *T. aestivum* (AABBDD genome) is thought to have arisen through hybridization of *T. turgidum* with the wild wheat species *Aegilops tauschii* Coss. (DD genome) (Kihara 1944, McFadden and Sears 1944). *T. zhukovskyi* (AAAAGG genome) originated through hybridization of *T. timopheevii* with cultivated einkorn *T. monococcum* in the Transcausus. To date, no wild forms are known for either *T. aestivum* or *T. zhukovskyi*. This and other lines of evidence indicate that these hexaploid species are in part cultivars (Kihara 1966, Dorofeev 1966, Dvorak et al. 1993).

The separate origins for the AABB and AAGG genome tetraploid species provide the framework for *Triticum* evolution. There are two polyploid lineages in the genus: the *T. turgidum* lineage (consisting of *T. turgidum* and *T. aestivum*) and the *T. timopheevii* lineage (consisting of *T. timopheevii* and *T. zhukovskyi*) (Fig. 2). Of these, the *T. timopheevii* lineage has limited distribution and its cultivars are endemic to the Transcausus. Unfortunately, relatively few evolutionary studies have been performed on this interesting group of wheats and much remains to be addressed concerning the details of their domestication and diversification. In contrast, bread wheat (*T. aestivum* L. subsp. *aestivum*) and other cultivars of the *T. turgidum* lineage are widespread and now produced globally. In addition, *T. turgidum* and *T. aestivum* have been important materials for cytological, genetic and breeding studies, and the major part of our current knowledge about polyploid wheat evolution comes from studies on these species. For this reason, I focus on the *T. turgidum* lineage in the following sections and summarize what is known and what has yet to be discovered about the course of its evolution.
Domestication of emmer wheat: when, where and how many times?

The evolution of the *T. turgidum* lineage wheats as crops was initiated when wild emmer wheat (*T. turgidum* subsp. *dicoccoides*) was brought into the process of domestication. Domesticated emmer wheat (*T. turgidum* subsp. *dicoccon*) was the product of this initial process. Today, natural stands of wild emmer wheat occur widely across the arc of the Fertile Crescent and they form two genetically distinct populations: southern (including Israel, Palestine, Lebanon and southwestern Syria) and northern (including Turkey, Iraq and Iran) populations (Valkoun et al. 1998, Luo et al. 2007). The question of when, where and how many times wild emmer wheat was domesticated is a long-standing issue. This question has an important relevance to our understanding of the origins of agriculture because the transition during the Neolithic period from the hunter–gatherer lifestyle to one that included farming was founded on the domestication of cereal crops such as emmer wheat, einkorn wheat (*T. monococcum* subsp. *monococcum*) and barley (*H. vulgare* L.).

Archaeological evidence indicates that emmer wheat was domesticated in the Fertile Crescent region ~10,000 years ago. The oldest remains of domesticated emmer wheat were found in Tell Aswad, Syria and date to ~9,800–9,300 years before present (Fig. 1). In addition, the remains of domesticated emmer wheat have been found from several other pre-pottery Neolithic sites in the Fertile Crescent region. Interestingly, domesticated emmer wheat seems to have appeared almost simultaneously in the southern and northern parts of the Fertile Crescent region during the period ranging from 9,500 to 9,000 years before present (Nesbitt and Samuel 1996, Feldman and Kislev 2007). This fact may suggest a northern origin of domesticated emmer wheat with its immediate spread to the south or vice versa. Alternatively, emmer wheat might have been domesticated independently from the southern and northern wild populations. With the records of archaeological remains alone, it is difficult to determine where the process of domestication was first initiated.

Genetic analyses provide an alternative approach to address the question of the beginnings of wheat domestication. In general, population genetic analyses offer the possibility of...
Table 1 The nomenclature of wild and cultivated *Triticum* wheats (after Van Slageren 1994*)

| Section       | Species and subspecies                  | Genome constitution | Examples of common names*  
|---------------|-----------------------------------------|---------------------|---------------------------
| Monococcon    | *Triticum monococcum* L.                | AA                  | Wild einkorn              
|               | subsp. aegilopoides (Link) Thell.       |                     | Cultivated einkorn        
|               | subsp. monococcum                       |                     |                           
| *Triticum urartu* Tumanian ex Gandilyan | AA                  |                     |                           
| Dicoccoidea   | *Triticum turgidum* L.                  | AABB                | Wild emmer                
|               | subsp. dicocoides (Körn. ex Asch. & Graebn.) |         | Cultivated emmer          
|               | subsp. dicoccon (Schrank) Thell.        |                     |                           
|               | subsp. durum (Desf.) Husn.              |                     | Durum or macaroni wheat   
|               | subsp. polonicum (L.) Thell.            |                     | Polish wheat              
|               | subsp. turanicum (Jakubz.) Å. Löve & D. Löve |               | Khorassan wheat           
|               | subsp. turgidum                         |                     | Rivet wheat               
|               | subsp. carthlicum (Nevski) Å. Löve & D. Löve |               | Persian wheat             
|               | subsp. paleoalbicicum (Menabde) Å. Löve & D. Löve | | Georgian wheat           
|               | *Triticum timopheevii* (Zhuk.) Zhuk.    | AAGG                | Wild timopheevii          
|               | subsp. armeniacum (Jakubz.) van Slageren |                     | Cultivated timopheevii    
|               | subsp. timopheevii                      |                     |                           
| Triticum      | *Triticum aestivum* L.                  | AABBD               | Common wheat              
|               | subsp. aestivum                         |                     | Bread wheat               
|               | subsp. compactum (Host) MacKey           |                     | Club wheat                
|               | subsp. sphaerococcum (Percival) MacKey  |                     | Indian dwarf wheat        
|               | subsp. macha (Dekapr. & Manabde) MacKey |                     |                           
|               | subsp. spelta (L.) Thell.               |                     | Spelt                     
|               | *Triticum zhukovskyi* Menabde & Ericz.  | AAAAGG              |                           

* For other taxonomic classifications, see the Wheat Classification Table Site (http://www.k-state.edu/wgrc/Taxonomy/taxintro.html).  
* Provided only when available.

![Diagram](https://academic.oup.com/pcp/article-abstract/52/5/750/1825619)

Fig. 2 Overview of the diversification of the *Triticum* wheats. The red arrows indicate the allopolyploidization events that involved the *Aegilops* species shown at the bottom, whereas the green arrow indicates the allopolyploidization event that involved the *Triticum* species. The vertical black arrows denote the domestication events. The *T. turgidum* lineage that is focused on in this paper is highlighted in yellow.
comparing the genetic structures of a wild progenitor and its domesticated counterpart to find the wild population with the closest relationship to domesticated populations. The locality where this wild population now grows can be identified as the site of domestication on the assumption that the wild progenitor has not experienced significant changes in geographical distribution or genetic structure since the divergence of the domesticated counterpart. On the basis of this rationale, the domestication site of emmer wheat has been sought through molecular marker analyses to detect amplified fragment length polymorphisms (AFLPs) (Özkan et al. 2002, 2005), chloroplast DNA (cpDNA) microsatellite variations (Mori et al. 2003) and restriction fragment length polymorphisms (RFLPs) (Luo et al. 2007).

The results of these molecular population genetic studies agree that the northern populations had an important role in the domestication of emmer wheat, although evidence for the site of domestication remains inconclusive. The AFLP and RFLP studies indicate that the Karacadag (or Diyarbakir) region in southeastern Turkey is a likely place for emmer wheat domestication. Importantly, this region lies within the Fertile Crescent’s small core area where agriculture is thought to have emerged through domestication of the Neolithic founder crops, namely einkorn wheat, emmer wheat, barley, lentil, pea, bitter vetch and chickpea (Lev-Yadun et al. 2000) (Fig. 1). This finding indicates the importance of the Karacadag Neolithic sites (such as Cayönü, Cafer Höyük and Nevali Çorî) as probable sites of emmer wheat domestication. However, it is still not certain that the Karacadag region was the sole place of domestication. The cpDNA microsatellite and AFLP studies suggest that the northern wild emmer populations that grow outside the core area participated in the process of domestication. Furthermore, Luo et al. (2007) pointed out that, although it is a less likely possibility, independent domestication in the southern Levant is not ruled out by the RFLP evidence.

From brittle to non-brittle rachis: an essential morphological change under domestication

Several morphological and physiological traits, including large fruits, increased apical dominance, loss of seed dormancy, and synchronized growth and flowering, distinguish crops from their wild progenitors. To meet human needs, such crop-specific traits developed through genetic modifications of wild plants. At the same time, those traits are important for crop plants in terms of adaptation to agroecological environments. For a given crop, there is a suite of traits that was supposedly selected for in the early stage of its domestication from the wild progenitor. Such traits and the genes that are responsible for their expression are referred to as domestication traits and domestication genes. In cereal crops, a common domestication trait is the loss of natural seed dispersal, which results in the seeds being retained in the spike and facilitates their harvest.

Domesticated emmer wheat is not capable of scattering seeds, because its non-brittle rachis (i.e. the main axis of the spike) does not spontaneously break at maturity. Genetic studies showed that the non-brittleness rachis is controlled by recessive alleles at two major loci, Brittle rachis-A1 (Br-A1, formerly known as Br2) and Brittle rachis-B1 (Br-B1, formerly known as Br3) that are located respectively on the short arm of chromosomes 3A and 3B (Watanabe et al. 2002). This evidence suggests that the non-brittle state of the rachis was established in the domesticated population through selection for the recessive alleles of these loci. The mutations that gave rise to the recessive alleles might have occurred in the process of domestication. Alternatively, the selected alleles might have been derived from wild emmer wheat, because, notwithstanding its strong negative adaptive nature, the non-brittle rachis phenotype is observed in wild emmer wheat populations (Kamm 1974). Comparative molecular marker mapping analyses confirmed that Br-A1 and Br-B1 are located in homoeologous regions of chromosomes 3A and 3B (Watanabe et al. 2005, 2006, Nalam et al. 2006). Interestingly, the major brittle rachis loci of barley, Br1 and Br2, are also located on the short arm of the homoeologous group 3 chromosome (3H) (Takahashi and Hayashi 1964, Komatsuda and Mano 2002). Whether or not the Br and Br loci are orthologous, however, has yet to be clarified (Nalam et al. 2006, Li and Gill 2006).

Post-domestication diversification: emergence of free-threshing tetraploid wheats

After its birth in the Fertile Crescent, domesticated emmer wheat spread widely across the Near East and beyond. By the seventh millennium before present, emmer wheat cultivation expanded eastward through the Mesopotamian plain to India, and westward through Anatolia to the Mediterranean coastal region and Europe. In these regions, it was one of the most prominent crops for almost 6,000 years (Zohary and Hopf 2000, Feldman and Kislev 2007). Domesticated emmer wheat underwent considerable varietal diversification in response to the particular agroecological conditions of the cultivation area (Table 1). The present-day cultivar known as durum wheat (T. turgidum subsp. durum) may have derived from domesticated emmer wheat in the eastern Mediterranean region (Feldman and Kislev 2007, Luo et al. 2007). Today, durum wheat, which is grown under relatively dry conditions and consumed as macaroni and semolina products, is the most widely cultivated tetraploid wheat.

Both wild and domesticated emmer wheat have tough glumes and hulled seeds that require hard threshing to allow the grain to be harvested. In contrast, durum wheat and its related forms, such as Rivet wheat (T. turgidum L. subsp. turgidum), Polish wheat [T. turgidum L. subsp. polonicum (L.) Thell.], and Khorasan wheat [T. turgidum L. subsp. turanicum (Jakubz.) Á.Löve & D.Löve], are free-threshing, i.e. easy-harvest wheats, thanks to their soft glumes and non-hulled seeds (Fig. 3).
The results of the genetic studies suggest that a genotypic change from \( qqTgTg \) to \( QQQtgt \) was essential to the emergence of the free-threshing phenotype in tetraploid wheats. Since \( Tg \) conceals the action of \( Q \), the dominant \( Q \) allele might have been present in domesticated emmer wheat, e.g. as the \( QQQtgTg \) genotype, without having any significant influence on the threshability phenotype. This view is supported by the existence of a domesticated emmer wheat variety, \( T. turgidum \) L. subsp. \textit{dicoccon} (Schrank) Thell. var. \textit{liguliforme} Körn. that carries the \( Q \) allele (Muramatsu 1979, 1985) (Fig. 3). One important question concerning the emergence of free-threshing wheats is whether the \( tg \) and \( Q \) alleles arose in tetraploid wheats or independently in tetraploid and hexaploid wheats. The recent molecular cloning of \( Q \) provides insight into the origin of this allele (Faris et al. 2003, Simons et al. 2006). According to those studies, the \( Q \) gene belongs to the AP2 family of transcription factors. The \( Q \) and \( q \) alleles differ by a single amino acid and the \( Q \) allele is more abundantly transcribed than \( q \) in developing spikes and other tissues. Comparative sequence analyses show that the \( q \) to \( Q \) mutation occurred only once in the evolution of \textit{Triticum} and precludes the possibility of independent origin of the \( Q \) allele in tetraploid and hexaploid wheats. The \( Q \) allele, therefore, might have originated in domesticated emmer wheat and given rise to \( Q \)-carrying varieties such as \( T. turgidum \) subsp. \textit{dicoccon} var. \textit{liguliforme}. Alternatively, the \( Q \) allele might have first appeared in hexaploid wheats and introgressed into tetraploid wheats through interploidy hybridization as discussed below.

**Fig. 3** Spikes of \( T. turgidum \) wheats. (A) Domesticated emmer wheat (\( T. turgidum \) subsp. \textit{dicoccon} (non-free-threshing). (B) Domesticated emmer wheat carrying the dominant \( Q \) allele (\( T. turgidum \) subsp. \textit{dicoccon} var. \textit{liguliforme}) (non-free-threshing). (C) Durum wheat (\( T. turgidum \) subsp. \textit{durum}) (free-threshing). Bar, 1 cm.

A quantitative trait locus (QTL) analysis of segregants derived from a cross between durum and wild emmer wheat showed that the free-threshing phenotype is controlled by four loci (Simonetti et al. 1999). Two of the major QTLs, which each accounts for \( \sim 25\% \) of the phenotypic variation, correspond to the previously known threshability loci, \( Tg \) (tenacious glume) on the short arm of chromosome 2B, and \( Q \) on the long arm of chromosome 5A. At these loci, the partially recessive \( tg \) and the partially dominant \( Q \) alleles confer free-threshing. The interaction between these loci affects spike morphology: \( Tg \) is epistatic to \( Q \), and the \( QQQtgTg \) genotype has a non-free-threshing phenotype. The \( Tg \) locus controls glume toughness (Kerber and Rowland 1974), whereas the \( Q \) locus pleiotropically affects glume shape and toughness, spike length, plant height and spike emergence time (Muramatsu 1963, Kato et al. 1999, 2003). The genetic systems for the free-threshing phenotype are, therefore, somewhat complex.
Transcaucasus (Dorofeev 1966, Matsuoka et al. 2008b). From such mixed cultivation, hybrid swarms, i.e. interbreeding hybrid populations including parental species, F₁ and later-generation hybrids, and individuals backcrossed to one or both parental species, may result. In addition, wild wheat species can also be involved in hybrid swarms in regions where they naturally grow in and around the areas of wheat cultivation. Interploidy introgression in hybrid swarms is thought to have contributed to the diversification of the *T. turgidum* wheats by giving rise to two subspecies, Georgian wheat [*T. turgidum* L. subsp. *paleocolchicum* (Menabde) Á. Löve & D. Löve] and Persian wheat [*T. turgidum* L. subsp. *carthlicum* (Nevski) Á. Löve & D. Löve] (Fig. 4). Georgian wheat, which is endemic to Georgia, is non-free-threshing and distinct from domesticated emmer wheat in having broad compact spikes. Persian wheat, which is now grown narrowly in the Transcaucasus, is free-threshing and strikingly similar to *T. aestivum* in morphology. On the basis of genetic and morphological evidence, Georgian wheat is assumed to be a segregant from a hybrid cross between wild emmer wheat and *T. aestivum* (Dvorak and Luo 2001), whereas Persian wheat may be a segregant from a hybrid cross between domesticated emmer wheat and *T. aestivum* (Kuckuck 1979). Introggression from hexaploid wheats, therefore, seems to have been an important mechanism for the diversification and enrichment of the gene pool of *T. turgidum* wheats.

**Birth of hexaploid common wheat: further diversification of the polyploid *Triticum* wheats through allopolyploid speciation**

The *T. turgidum* wheats are genetically and morphologically diverse and the question of how they evolved under cultivation is intriguing in itself. However, it is perhaps their dispersal to new territories and subsequent natural interspecific hybridization that had the most profound impact on the development of human societies as well as on the evolution of cultivated wheats. In the accepted scenario for the allopolyploid speciation of hexaploid common wheat *T. aestivum* L. (AABBDD genome), the cultivated forms of *T. turgidum* migrated north-eastward in association with the spread of agriculture across and beyond the Fertile Crescent region. As a result of this human-mediated species range expansion, *T. turgidum* (AABB genome) came into contact with *Ae. tauschii* (DD genome) and the critical natural hybrid cross that led to the allopolyploid speciation of common wheat took place in an agroecological environment. This scenario is based on two facts. Firstly, the well-established genetic theory for the origin of common wheat points to *T. turgidum* and *Ae. tauschii* respectively as the female and male progenitors of *T. aestivum* (Kihara 1944, McFadden and Sears 1944). Secondly, no wild form of *T. aestivum* has ever been found, indicating that cultivated *T. turgidum* hybridized with *Ae. tauschii* (Kihara 1966).

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**Fig. 4** Evolution of the *T. turgidum*–*T. aestivum* complex. The orange and green shading respectively indicate non-free-threshing and free-threshing wheats. The interploidy hybridization and introgression events that involved *Ae. tauschii* (red arrows) and wild or domesticated emmer wheat (blue arrows) are shown. The dashed red arrow denotes the possible but not confirmed pathway for the origin of Asian spelt wheat, whereas the dashed yellow arrow denotes the possible but less likely diversification pathway from spelt wheat to the free-threshing *T. aestivum* wheats.
The birth of common wheat presents a marked stage of the diversification continuum (i.e. a continuous process of diversification) of the polyploid *Triticum* wheats. The questions of where and how many times the allopolyploid speciation of *T. aestivum* took place, however, have yet to be answered. *Ae. tauschii* has a wide natural species range in central Eurasia, spreading from northern Syria and southeastern Turkey to western China with its center of genetic and morphological diversity in the Transcaucasus and the southern Caspian coastal region (Tanaka and Tsujimoto 1991, Van Slageren 1994, Dvorak et al. 1998, Matsuoka et al. 2008a, 2009, Takumi et al. 2009 for correction, Mizuno et al. 2010b) (Figs. 1, 5). Comparative analyses of DNA variation indicate that a northeastern portion of the Fertile Crescent and its neighboring regions of Transcaucasus and the southern coastal Caspian are the most likely areas of the original allopolyploidization events, because the *Ae. tauschii* populations of that area are genetically more similar to the D genome of *T. aestivum* than those of other areas (Dvorak et al. 1998, Lelley et al. 2000, Giles and Brown 2006). In addition, molecular genetic data suggesting that allopolyploidization is a recurring process during *T. aestivum* evolution are increasing (Talbert et al. 1998, Caldwell et al. 2004). The hexaploid common wheat is probably the product of multiple allopolyploid speciation events that took place in the western peripheral region of the natural range of *Ae. tauschii* (Fig. 1). The earliest record of hexaploid wheat is from southeastern Turkey (8,600–7,800 years before present), consistent with the idea that *T. aestivum* first arose in that area (Hillman 1978, Nesbitt 2001).

**T. turgidum–*Ae. tauschii* natural hybridization**

The scenario described above for the hybrid origin of *T. aestivum* is widely accepted; however, several questions remain to be addressed. The scenario assumes three critical reproductive and genetic events through which successful allopolyploid speciation was brought about: *T. turgidum–* *Ae. tauschii* natural hybridization, normal growth of fertile triploid F₁ hybrids and genetic and epigenetic changes in the allohexaploid genomes of the F₂ and later generations (Fig. 6). The first of these, natural hybridization between *T. turgidum* and *Ae. tauschii*, is of particular importance as it represents the platform for the allopolyploid speciation. Field studies have shown that cultivated *T. turgidum* and *Ae. tauschii* grow together in some districts of Iran (Kihara et al. 1965, Matsuoka et al. 2008b). To my knowledge, however, no natural *T. turgidum–* *Ae. tauschii* hybrid has ever been reported, despite the fact that natural intergeneric hybrids between *Aegilops* and *Triticum* species are commonly observed in Middle Eastern wheat fields (Van Slageren 1994, 757 Planta...
Y. Matsuoka, unpublished observation). Since each progenitor of *T. aestivum* is a reproductively isolated biological species, some ecological barriers, for example, flowering time differences, may interfere with the occurrence of natural hybridization under current field conditions. In addition, some genetic factors might be involved as determining factors for successful crosses between *T. turgidum* and *Ae. tauschii*, because, in the case of the wheat–rye (*Secale cereale* L.) cross, the intergeneric crossability is known to be affected by *Kr* genes (Riley and Chapman 1967, Manickavelu et al. 2009). Under what ecologic-al and genetic conditions did *T. turgidum* and *Ae. tauschii* naturally hybridize ~8,000 years ago? Further field and laboratory studies will be required to better understand the ecological and genetic factors that influenced the hybridization.

**Normal growth of fertile triploid F1 hybrids: unreduced gamete production and hybrid abnormalities**

The normal growth shown by fertile triploid F1 hybrids between *T. turgidum* and *Ae. tauschii* has strong relevance to allopolyploidization per se, because it is in this generation that the genome doubling from triploid to hexaploid is believed to have taken place (Fig. 6). In general, allopolyploid speciation, which results from hybridization and genome doubling, has long been recognized as an important mode of hybrid speciation in plants (Soltis and Soltis 2009). In this process, genome doubling may occur via either somatic chromosome doubling or the union of unreduced gametes whose chromosome number is equivalent to that of the parental somatic cells. The latter is thought to be the route for speciation of most allopolyploid plants including *T. aestivum* (Harlan and De Wet 1975). In spite of the importance of unreduced gametes in allopolyploid speciation, the details of their mechanism of production have yet to be elucidated. At present, very little is known about the extent of the influence of genetic or environmental factors on unreduced gamete production in hybrid plants. In contrast, in some non-hybrid plants, unreduced gamete production is controlled by relatively simple genetic systems (Rhoades and Dempsey 1966, Mok and Peloquin 1975, d’Erfurth et al. 2009).

*T. aestivum* and its progenitors may provide a useful model system for studying the mechanisms that underlie unreduced gamete formation in hybrid plants. The natural processes of unreduced gamete production can be reproduced in artificial triploid F1 hybrid plants that are produced from crosses between *T. turgidum* and *Ae. tauschii* without the use of chemicals or embryo rescue techniques (Kihara and Lilienfeld 1949, Matsuoka and Nasuda 2004, Cai et al. 2010) (Fig. 5). In *T. turgidum–Ae. tauschii* triploid F1 hybrids (2n = 21), unreduced gametes are produced through a non-reductional meiosis (Fig. 7). Unlike normal meiosis, non-reductional meiosis involves a single mitosis-like cell division. As a result, symmetrical dyad daughter cells, each of which has 21 chromosomes, are produced from a triploid gametocyte. Non-reductional meiosis is thought to occur in both male and female gametogenesis and the union of unreduced gametes results in the formation of hexaploid zygotes (2n = 42). Formation of gametes by non-reductional meiosis enables *T. turgidum–Ae. tauschii* triploid F1 hybrids to set seeds and be fertile despite the haploid status of their genomes. The seed set rates of selfed *T. turgidum–Ae. tauschii* triploid F1 hybrids can be as high as 70% depending on the genotype of the parents and the environmental conditions (Kihara et al. 1965, Fukuda and Sakamoto 1992a, b, Matsuoka et al. 2007).

Morphological and physiological abnormalities, including hybrid necrosis and hybrid chlorosis, can affect the growth of the *T. turgidum–Ae. tauschii* triploid F1 hybrids (Nishikawa 1960, 1962a, b). In contrast to unreduced gamete formation, these hybrid abnormalities have a negative effect on the allopolyploid speciation of *T. aestivum*, because they reduce fertility in the *T. turgidum–Ae. tauschii* triploid F1 hybrids. Analysis of crosses between a *T. turgidum* cultivar and *Ae. tauschii* accessions showed that the occurrence of abnormalities in the triploid F1 hybrids was restricted to accessions from a limited geographical area, indicating that post-zygotic hybridization barriers between these species are still under development (Matsuoka et al. 2007). Other studies showed that expression of hybrid abnormalities are under genetic control; however, molecular genetic approaches have only recently been used to study the genetic mechanisms underlying these phenomena. Detailed analyses of the *T. turgidum–Ae. tauschii* triploid F1 hybrids have shown that, in necrotic hybrid plants, an autoimmune response occurs as the result of an epistatic interaction of genes derived from the parental species (Mizuno et al. 2010a).

**Genetic and epigenetic changes in the allohexaploid genomes of F2 and later generations**

The outlined scenario for the hybrid origin of *T. aestivum* assumes the formation of AABBD genome allohexaploid plants through merger of the AABB (from *T. turgidum*) and DD (from *Ae. tauschii*) genomes (Fig. 6). The merger of two evolutionarily distinct genomes in the same nucleus during the process of allopolyploidization may cause chromosome instability in subsequent generations (McCintock 1984). In newly hybridized wheat plants, aneuploid offspring are produced by AABBD genome F2 euhexaploids that show regular diploid-like chromosome behavior in meiosis and have high fertility (seed set rate >80%) (Kihara and Lilienfeld 1949). Univalent chromosomes are present at metaphase I of meiosis and are associated with the production of aneuploid gametes; however, the cause of this abnormal meiotic chromosome behavior remains unclear. The extent of chromosomal instability is affected by the genotypes of the AB and D genome progenitors, suggesting that...
some genetic factor is involved in production of aneuploid offspring by newly hybridized euhexaploid plants (Tabushi 1964, Mestiri et al. 2010). Aneuploidy does occur in the natural varieties of common wheat (Riley and Kimber 1961), but the frequency is much higher in new allohexaploids. Selecting or modifying genetic factors for stable chromosome transmission, therefore, must have been part of the successful speciation of T. aestivum.

In plants, it has been shown that newly formed polyploid species undergo genomic restructuring through the movement of transposable elements, rapid changes in gene expression patterns and elimination of genomic DNA (Adams and Wendel 2005). These processes are thought to provide the sources of novel genetic variation that may drive phenotypic and ecological diversification in polyploid plants. In newly hybridized AABBDD genome allohexaploid plants, several studies have found that genomic DNA elimination and gene silencing occur in the early generations (Özkan et al. 2001, He et al. 2003, but see Shitsukawa et al. 2007). Furthermore, elimination of an Ae. tauschii allele was observed during development of a second-generation allohexaploid embryo, suggesting that genomic DNA elimination may occur in a tissue-specific manner (Khasdan et al. 2010). Nevertheless, the fundamental issues of what genetic mechanisms control genomic DNA elimination and gene silencing and whether those DNA level changes are associated with chromosomal instability (i.e. the occurrence of aneuploidy) are yet to be addressed.

### Post-speciation diversification of common wheat

Through the addition of the D genome, T. aestivum acquired an adaptive capacity to a wide range of environmental conditions including large variations in summer humidity and winter coldness, and short photoperiodicity (Dubcovsky and Dvorak 2007). The broad adaptability of T. aestivum facilitated its spread to the humid eastern Asia and cold central and northern Europe. Across this wide distribution range in Eurasia, T. aestivum diversified and evolved numerous landraces under local conditions of cultivation, resulting in the formation of the five taxonomically recognized subspecies (Table 1).

In parallel with the case of the T. turgidum wheats, there are two distinct forms of common wheat in terms of threshability: firstly, the free-threshing subspecies T. aestivum L. subsp. aestivum, T. aestivum L. subsp. compactum (Host) MacKey and T. aestivum L. subsp. sphaerococcum (Percival) MacKey; and secondly, the non-free-threshing subspecies T. aestivum L. subsp. macha (Dekapr. & Menabde) MacKey and T. aestivum L. subsp. spelta (L.) Thell. (Table 1). Molecular mapping of loci that affect the threshability trait of common wheat identified two major QTLs, one on the short arm of chromosome 2D and the other on the long arm of chromosome 5A (Jantasuriyarat et al. 2004). The QTL located on 5A corresponds to the Q gene (Muramatsu 1963), whereas the QTL located on 2D corresponds to the gene known as Tg that inhibits the expression of Q (Kerber and Rowland 1974). The study additionally identified the Tg gene on
the short arm of chromosome 2B (Simonetti et al. 1999) as a significant QTL. In common wheat, the Tg gene on chromosome 2D, which originally derived from Ae. tauschii, has a predominant effect on the expression of the free-threshing phenotype (Jantasuriyarat et al. 2004).

The advances in understanding the genetic mechanisms for expression of the free-threshing trait have enabled elaboration of the model for common wheat evolution and diversification and provided a picture of how free-threshing and non-free-threshing forms evolved (Fig. 4). The genotype of free-threshing common wheats can be designated QQ\text{tg}TgTg\text{2D}, because they have mutant alleles at each of the three important threshability loci: Q on chromosome 5A, Tg on chromosome 2B and Tg on chromosome 2D. On the basis of this genotype designation, the most parsimonious model for the evolution of the free-threshing phenotype hypothesizes that the tetraploid progenitor of free-threshing T. aestivum is free-threshing T. turgidum with a QQ\text{tg}TgTg\text{2D} genotype. In this model, a single recessive Tg to tg mutation at the locus on chromosome 2D is assumed to provide the free-threshing phenotype of common wheat. This single mutation model predicts relatively early emergence of the free-threshing phenotype after allopolyploid speciation and is consistent with the observation that the earliest T. aestivum remains from southeastern Turkey (8,600–7,800 years before present) are from the free-threshing form. In addition, the absence of archaeological evidence for non-free-threshing common wheat in the Near East and Transcaucasus is consistent with the idea that the hexaploid with the QQ\text{tg}TgTg\text{2D} genotype was a transient form that existed for a short period prior to the emergence of free-threshing common wheat (Hillman 1978, Nesbitt and Samuel 1996, Nesbitt 2001).

Another possible, but less likely, model for the evolution of the free-threshing phenotype hypothesizes that the free-threshing form evolved from non-free-threshing common wheat (McFadden and Sears 1946). In this model, multiple mutations at the threshability loci would be required for the emergence of the free-threshing phenotype, because non-free-threshing common wheat is expected to have the qq\text{tg}TgTg\text{2D} genotype (MacKey 1954, 1966, but see Luo et al. 2000). The polygenic system of the non-free-threshing phenotype, therefore, seems to have served as a genetic barrier to the evolution of the free-threshing phenotype.

Interploidy natural hybridization and subsequent introgression had a significant role in the diversification of common wheat, similarly to the T. turgidum wheats (Dvorak et al. 2006). This is particularly the case for non-free-threshing common wheats (Fig. 4). Spelt wheat (T. aestivum subsp. spelta) (Fig. 5) has two landrace groups: European and Asian spelt wheats (Kuckuck 1959). European spelt wheat was traditionally cultivated in Germany, Switzerland and France, whereas Asian spelt wheat was collected from Iran, the Transcaucasus, Afghanistan and Tajikistan (Dorofeev 1966, Perrino et al. 1996, Dedkova et al. 2004). European spelt wheat was once considered as the progenitor of free-threshing T. aestivum (McFadden and Sears 1946); however, later comparative genetic studies indicated that European spelt wheat arose through the introgression of cultivated emmer wheat into free-threshing T. aestivum (MacKey 1966, Tsunewaki 1968, Blatter et al. 2004, Hiroawa et al. 2004). The origin of Asian spelt wheat remains elusive. Macha wheat (T. aestivum subsp. macha) provides another example of common wheat diversification through interploidy introgression. This cultivar is endemic to Georgia and is cultivated along with tetraploid Georgian wheat (T. turgidum subsp. paleocolchicum) (Jakubziner 1958, Dorofeev 1966). Comparative and molecular genetic analyses suggest that macha wheat is a segregant from a hybrid cross between wild emmer wheat and T. aestivum. It is likely that macha and Georgian wheats are sibling cultivars that arose in a hybrid swarm involving T. aestivum and wild emmer wheat (Tsunewaki 1968, Dvorak and Luo 2001).

Conclusions

In this paper, the evolution of polyploid Triticum wheats under cultivation is viewed as a diversification continuum, in which wild emmer wheat resides at one end and common wheat at the other, rather than as a collection of discrete evolutionary processes that separately proceeded at the tetraploid and hexaploid levels. The process of continuous diversification was initiated by domestication of emmer wheat and driven by several events of natural hybridization and allopolyploid speciation that took place in agroecological environments. The genetic evidence that has been accumulated over the past five decades show the reticulate nature of polyploid Triticum wheat evolution, as exemplified by the fact that interploidy hybridization between T. turgidum and T. aestivum is supposed to be involved in the origins of two of the eight subspecies of T. turgidum and two of the five subspecies of T. aestivum. In the wheat field, hybrid swarms can occur when various cultivars are grown in a mixture, and introgression between T. turgidum and T. aestivum probably occurred more frequently than previously thought. Such hybrid swarms likely were the cradle for the diversification of the T. turgidum–T. aestivum complex.

Review of previous studies has made it clear that a number of issues remain to be addressed regarding the evolution of the polyploid Triticum wheats. The diversification continuum view highlights the fact that there are several critical, but underappreciated, questions concerning the allopolyploid speciation of T. aestivum that remain unanswered. For example, to what extent did the genotypes of T. turgidum and Ae. tauschii influence allopolyploid speciation of T. aestivum? What genetic mechanisms underlie unreduced gamete production in triploid F1 hybrids? How are naturally forming AABBDD genome plants genetically stabilized during allopolyploidization? These questions are particularly interesting because they have direct relevance to the understanding of mechanisms for hybrid speciation in plants.
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