Chapter 18
Wheat Domestication: Key to Agricultural Revolutions Past and Future

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Contents

Abstract The domestication of wheat was instrumental in the transition of human behavior from hunter-gatherers to farmers. It was a key event in the agricultural revolution that occurred about 10,000 years ago in the Fertile Crescent of the Middle East. Transitions of forms with natural seed dispersal mechanisms to forms with non-brittle rachises led to the domestication of diploid einkorn and tetraploid emmer wheat in southeast Turkey. These early domesticates were staple crops of early farmers for several thousand years before being replaced by free-threshing wheats. Allopolyploidization, mutations in genes governing threshability and other domestication related traits, and interspecific gene flow led to the formation of today's economically important bread wheat. Genetics, genomics, and archaeobotany have together

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provided strong evidence and insights regarding the time, place, and events involved in the evolution and domestication of modern wheat, but numerous questions remain unanswered. Here, I review historical and recent findings that have shaped our current understanding of wheat domestication. Whole-genome sequence analysis, additional genetic studies, and advances in archaeology will likely address our unanswered questions in the future. A thorough and comprehensive understanding of wheat evolution and domestication will provide critical knowledge to the spawning of a new agricultural revolution, which will be necessary to provide sustenance for a rapidly increasing world population under global climate change.

Keywords Wheat · Durum · Einkorn · Emmer · Triticum · Aegilops · Evolution · Domestication · Fertile crescent · Brittle rachis · Tenacious glume · Q gene

18.1 Introduction

Before 10,000 years ago, man lived a nomadic life style as a hunter-gatherer relying on the hunting of wild animals and collecting wild plants for his food. Then, the Neolithic revolution took place where the hunter-gatherer way of life was replaced by an agrarian lifestyle. This was a crucial turning point in human history and had a profound effect on life thereafter. The Neolithic revolution took root in the Levantine Corridor and spread through the Fertile Crescent, which is located in the Middle East and encompasses a region extending from Jordan, Israel, Lebanon, and Syria through southeast Turkey and along the Tigris and Euphrates rivers through Iraq and western Iran (Fig. 18.1). This "cradle of agriculture" was the center of domestication of einkorn (*Triticum monococcum* L.) and emmer (*T. turgidum* ssp. *dicoccum* L.) wheat, which were staple crops of early civilization and close relatives of modern day wheat. These cereals were domesticated along side other important crops including barley (*Hordeum vulgare* L.), pea (*Pisum sativum* L.) Lentil (*Lens culinaris* Medikus), and chickpea (*Cicer arietinum* L.), as well as animals such as sheep (*Ovis aries*), goats (*Capra hircus*), cattle (*Bos taurus*), and pigs (*Sus scrofa*) (Zeder 2008), and they led the way for an agricultural revolution.

Nesbitt (2001) describes domestication as ". . . the process by which humans take reproductive control of plants or animals, modifying them for their own purposes." In wheat and other cereal crops, the first and most critical modification was the acquisition of a non-brittle rachis, which limited the natural seed dispersal mechanisms of the wild forms and allowed early farmers to harvest the grain much more efficiently without spikelets dropping to the ground prematurely and being lost. Other modifications included larger seeds, loss of seed dormancy, the free-threshing character, enhanced grain quality, and others (Harlan et al. 1973). These changes resulted in domesticated forms that relied on farmers for their propagation and also allowed mechanized cultivation on a large scale.

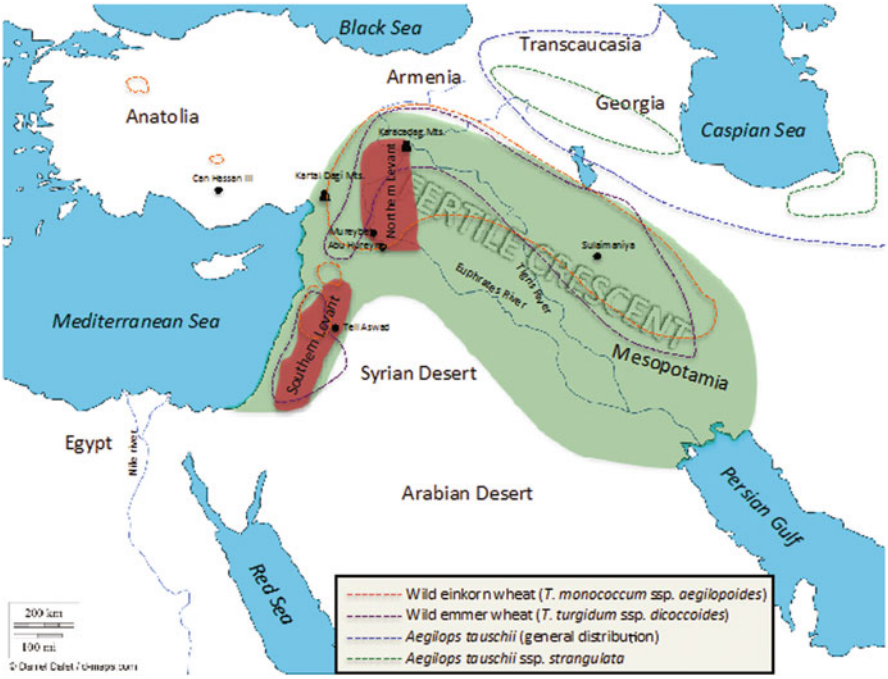

Fig. 18.1 Map of the ancient Middle East showing the Fertile Crescent (*green*). The Southern and Northern Levant regions are indicated by the *brown* shaded areas. Archaeological sites mentioned in the text are indicated by *black circles* (villages) and trapezoids (mountain ranges). The distributions of wild wheats are indicated by the *dotted lines* (see legend at the bottom of the figure). The basic map was obtained from d-maps.com. (http://d-maps.com/carte.php?lib=fertile_crescent_map&num_car=5852&lang=en)

Today, about 430 million tonnes of the fully domesticated free-threshing hexaploid and tetraploid wheats known as common, or bread, wheat (*T. aestivum* ssp. *aestivum* L.) and durum, or macaroni, wheat (*T. turgidum* ssp. *durum* L.), respectively, are produced annually and provide about a fifth of the calories consumed by humans worldwide (http://faostat.fao.org). Bread wheat accounts for about 95 % of the total wheat crop and is used to make bread, cookies, cakes, crackers, pastries, and noodles, whereas durum wheat accounts for the remaining 5 % and is used to make pasta and other semolina products. Due to the rate of the world's population growth, the demand for wheat is expected to increase by 40 % by 2030 (Dixon et al. 2009). In order to meet this demand, an annual increase in yield of 2 % is needed and the amount of agricultural land needs to be stabilized. These gains will need to come by way of genetic improvements and enhanced understanding of plant biology. Advancing our knowledge and understanding of wheat evolution and the genetic mechanisms underpinning the core domestication events that shaped today's wheat plant may provide new clues as to how the genetic diversity available in the wild wheat progenitors and relatives can be tapped into and exploited to initiate a modern agricultural revolution under a changing global climate.

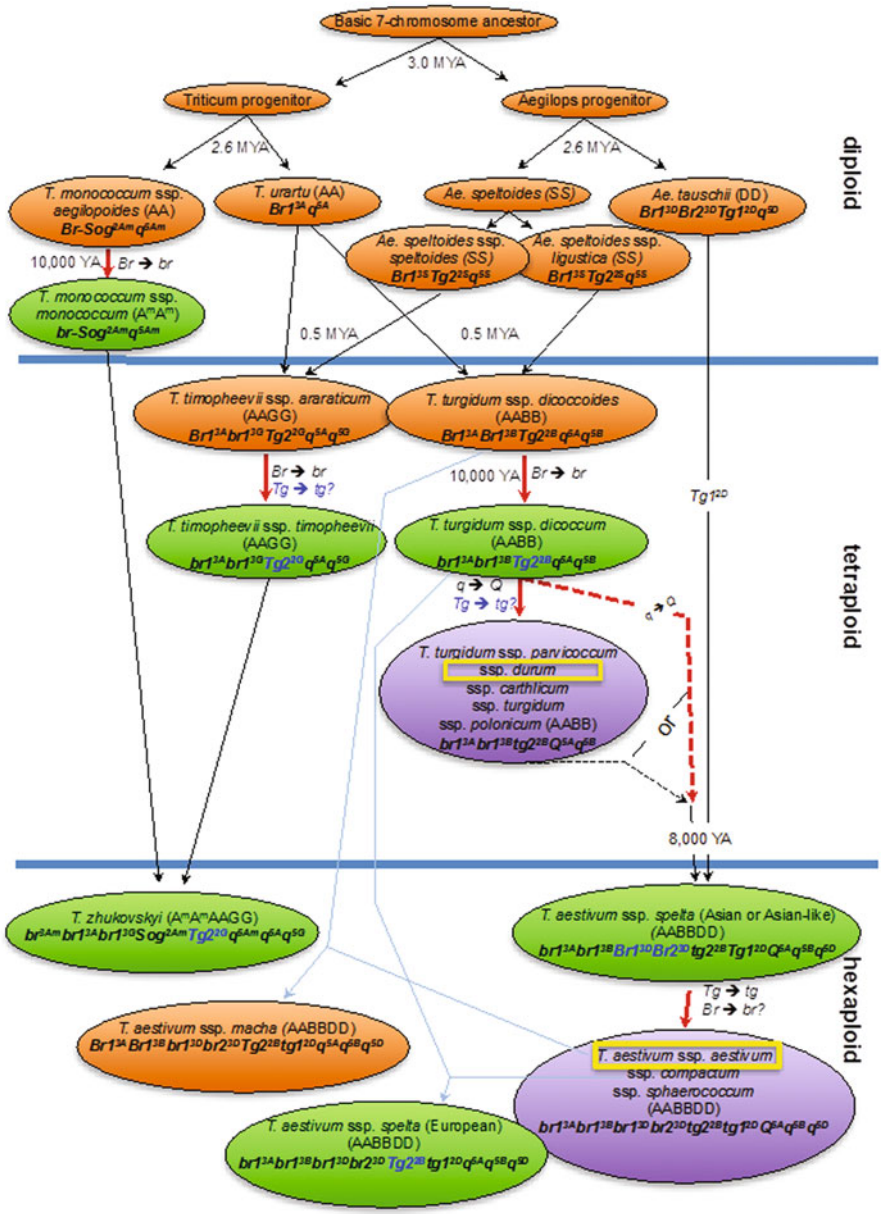

Fig. 18.2 The evolutionary lineages involving *Triticum* wheat species. The diploid, tetraploid, and hexaploid species are separated by *blue bars*. *Orange*, *green*, and *purple* colors indicate species with brittle rachis and hulled seed, species with non-brittle rachis and hulled seed, and species with a fully tough rachis and free-threshing seed, respectively. *Red arrows* indicate occurrences of transitions involving one or more of the major domestication genes *Br*, *Tg*, or *Q*. Genotypes of major domestication genes are indicated in bold below the taxonomical names and their genome

18.2 The Evolution of Wheat

It was determined nearly a century ago that the cultivated wheat species of the genus *Triticum* have chromosome numbers of $2n = 14$, 28, and 42. This indicated that the basic Triticeae genome was organized into seven chromosomes ($1x = 7$) and the various *Triticum* species consisted of diploids ($2n = 2x = 14$), tetraploids ($2n = 4x = 28$), and hexaploids ($2n = 6x = 42$) (Sax 1922; Kimber and Sears 1987).

The diploid progenitors and close relatives of modern wheat radiated from a common ancestor about 3 million years ago (MYA) and gave rise to the *Triticum* and *Aegilops* taxa (Fig. 18.2). The *Triticum* group consisted of the A-genome diploids *T. urartu* Tumanian ex Gandylian ($2n = 2x = 14$, AA (the capital letters represent the genome constitution)) and *T. monococcum* ssp. *aegilopoides* (Link) Thell. ($2n = 2x = 14$, AA). Johnson and Dhaliwal (1976) determined that they are valid biological species. Also evolving from the common seven-chromosome ancestor were numerous diploid *Aegilops* species including *Ae. tauschii* Coss. ($2n = 2x = 14$, DD) and a progenitor to the *Aegilops* Sitopsis section, which gave rise to the S-genome containing *Aegilops* species including *Ae. speltoides* Tausch ($2n = 2x = 14$, SS).

The only domesticated diploid wheat is einkorn (*T. monococcum* ssp. *monococcum* L., $2n = 2x = 14$, A^mA^m), which was domesticated from ssp. *aegilopoides* through the acquisition of a non-brittle rachis (Fig. 18.2). The evolution and formation of the cultivated forms of polyploid wheat followed two basic lineages, both of which involved two amphiploidization events. These events resulted from the hybridization of two different species followed by spontaneous chromosome doubling of the F_1 hybrid through the functioning of meiotic restitution division (non-reduced) gametes. One lineage began with hybridization of *T. urartu* (Dvorak et al. 1993) and *Ae. speltoides*, or a close relative thereof (Sarkar and Stebbins 1956; Riley et al. 1958), which led to the formation of the wild emmer wheat *T. timopheevii* ssp. *araraticum* Jakubz. ($2n = 4x = 28$, AAGG) containing a pair of A genomes from *T. urartu* and a pair of G genomes, which are considered to be a divergent form of the S genome of the *Aegilops* progenitor (Rodriquez et al. 2000). *T. timopheevii* ssp. *araraticum* has a brittle rachis conferred by the $Br1^{3A}$ gene. A mutation in $Br1^{3A}$ led to a non-brittle rachis and the domestication of this form to *T. timopheevii* ssp. *timopheevii* (Zhuk.) Zhuk ($2n = 4x = 28$, AAGG). *T. timopheevii* was never cultivated as a significant crop and grows only in a limited region of Georgia. Therefore, it was probably a secondary domesticate (Nesbitt and Samuel 1996).

The hexaploid wheat belonging to this lineage is *T. zhukovskyi* Menabde et Ericzjan ($2n = 6x = 42$, A^mA^mAAGG), which resulted from a hybridization between *T. timopheevii* ssp. *timopheevii* and domesticated einkorn wheat (Jakubziner 1958; Johnson 1968). Like ssp. *timopheevii*, *T. zhukovskyi* is not cultivated and tends to

Fig. 18.2 constitutions. Homozygosity is inferred at each locus, and genotypes are indicated only once to save space. Genotypes in *blue* are suggested but no experimental evidence is available. *Blue arrows* represent events that occurred to give rise to hexaploid subspecies that formed subsequent to *T. aestivum* ssp. *aestivum*. Durum and common wheat, the two modern widely cultivated forms of polyploid wheat, are highlighted with *yellow rectangles*

be found in Western Georgia as an admixture with *T. timopheevii* and einkorn wheat (Nesbitt and Samuel 1996). Although this constitutes an interesting evolutionary lineage of wheat, it did not result in the formation of any of today's economically important wheats. Therefore, little attention will be devoted to the species of this lineage in the remainder of this review.

Like the first lineage, the second also began with a hybridization event between *T. urartu* (Dvorak et al. 1993) and a close relative of *Ae. speltoides* (Dvorak and Zhang 1990; Blake et al. 1999; Huang et al. 2002; Chalupska et al. 2008; Salse et al. 2008) but one of a different subspecies than the one involved in the first lineage (Kilian et al. 2007; Fig. 18.2). This event led to the formation of the tetraploid wild emmer wheat *T. turgidum* ssp. *dicoccoides* (Körn.) Thell ($2n = 4x = 28$, AABB genomes). Although both wild emmer wheat species (*T. turgidum* spp. *araraticum* and *dicoccoides*) obtained a pair of genomes from the S genome-containing *Ae. speltoides*, significant divergence has since occurred such that the B, G, and S genomes, while still related, are quite distinct (Zhang et al. 2002; Kilian et al. 2007). Like ssp. *araraticum*, ssp. *dicoccoides* has a brittle rachis, and mutations in *Br* loci led to the domesticated emmer subspecies *T. turgidum* ssp. *dicoccum* (Schrank) Schübl ($2n = 4x = 28$, AABB genomes), which has a non-brittle rachis and hulled seed (Fig. 18.3). The second amphiploidization event of this lineage resulted when the diploid goat grass *Ae. tauschii* hybridized with a *T. turgidum* subspecies (Kihara 1944; McFadden and Sears 1946; Fig. 18.2). The resulting hexaploid was hulled due to the presence of the *Tg1* gene from *Ae. tauschii* (McFadden and Sears 1946). This subspecies may have been similar to Asian spelta (*T. aestivum* ssp. *spelta* L., $2n = 6x = 42$, AABBDD) (Figs. 18.2, 18.3). Evolution of this species through the acquisition of the free-threshing character (see below) resulted in the free-threshing hexaploid bread wheat *T. aestivum* ssp. *aestivum* L., $2n = 6x = 42$, AABBDD) (Figs. 18.2, 18.3), one of the most economically important crops in the world today.

Other hexaploid *T. aestivum* spp. include *compactum* (Host) MacKey, *sphaerococcum* (Percival) MacKey, *macha* Dekapr. et Menabde, and European *spelta* L. Subspecies *compactum* (club wheat) and *sphaerococcum* (shot wheat) are both free-threshing and differ from *aestivum* by single genes that arose through mutation. Ssp. *compactum* carries the *C* gene, which confers a compact spike and *sphaerococcum* carries the *S* gene for spherical grains. Ssp. *compactum* is grown today in a few isolated areas of Europe, the Near East, and the northwestern U.S., whereas *sphaerococcum* is confined mostly to India. Spp. *macha* and European *spelta* are not free-threshing and resemble primitive forms, but are not progenitors to *aestivum*. Ssp. *macha* likely arose through a more recent hybridization between *aestivum* and the emmer wheat *T. turgidum* ssp. *dicoccum* (Dvorak and Luo 2001), and there is now much evidence demonstrating that European *spelta* formed from a cross between *T. aestivum* ssp. *compactum* and domesticated emmer (*T. turgidum* ssp. *dicoccum*) (Bertsch 1943; MacKey 1966; Blatter et al. 2002, 2004; Yan et al. 2003; Fig. 18.2).

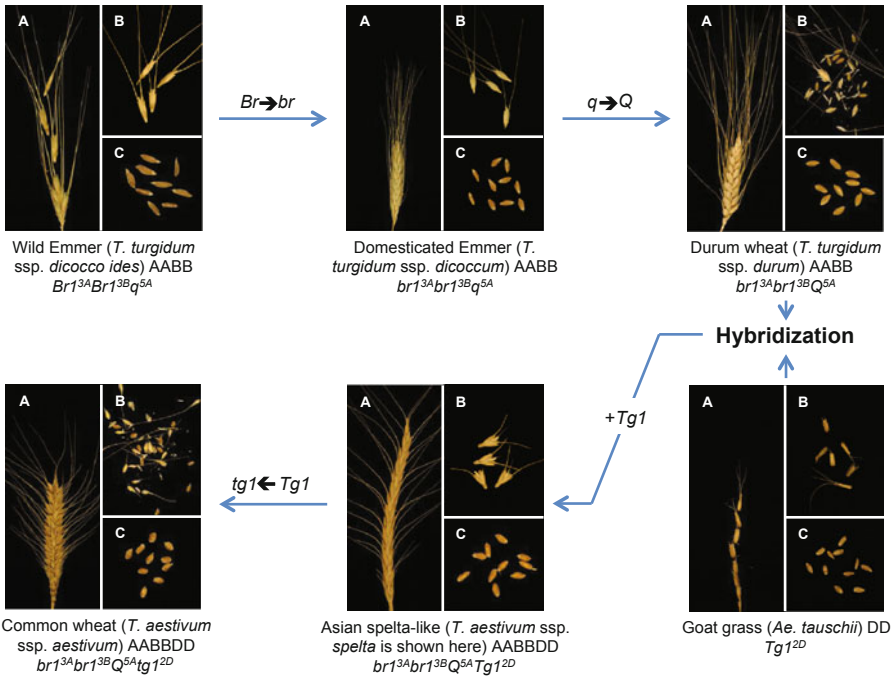

Fig. 18.3 The phenotypes of wheat species involved in the evolution of modern cultivated wheat and major transitions at the primary domestication genes ($Br1^{3A,\ 3B}$, q^{5A}, and $Tg1^{2D}$). The spike, result of moderate hand threshing, and seed are shown for each in panels A, B, and C, respectively. Although direct evidence is lacking, the most likely scenario in which a free-threshing (*Q*-containing) tetraploid hybridized with the D genome diploid *Ae. tauschii* to produce hexaploid wheat is shown. Also, Asian spelta is shown to represent the primitive progenitor to free-threshing common wheat because it is likely that the progenitor was very similar. The common names, taxonomical names, genome constitutions, and genotypes are indicated below each panel

18.3 The Place and Time of Einkorn and Emmer Wheat Domestication

Today, findings from archaeological digs combined with molecular genetics experiments have provided many answers regarding wheat domestication. Agriculture originated in the Fertile Crescent approximately 10,000 years ago, but the earliest gathering of wild emmer wheat has been dated to 19,000 years before present (BP) in the Middle East indicating that humans collected wild grains for some 10,000 years before domestication took place. Futhermore, Tanno and Willcox (2006) argue that cereals were actually cultivated for over a thousand years before the emergence of domesticates in what would be considered the first phase of cultivation. In the second phase of cultivation, domesticated forms consisting of einkorn and emmer wheat were grown by early farmers. These wheats acquired a non-brittle rachis, which allowed early farmers to efficiently harvest the grain without the spikes shattering and

falling to the ground before harvest. Later, further domestication occurred through the acquisition of the free-threshing character. This led to complete replacement of the hulled einkorn and emmer wheats with the free-threshing durum and bread wheat, although replacement was not rapid.

18.3.1 Domestication of Einkorn Wheat

Wild (*T. monococcum* ssp. *aegilopoides*) and domesticated einkorn wheat (*T. monococcum* ssp. *monococcum*) are very similar morphologically except that that the former has a brittle rachis and the latter a non-brittle rachis. The distribution of wild einkorn in the Middle East is rather widespread and is found from the Balkans to Iran primarily in the northern and eastern parts of the Fertile Crescent growing as a weed along roadsides and fields (Nesbitt and Samuel 1996; Fig. 18.1). Man collected grains of wild einkorn for some time before cultivating it, because brittle-rachis einkorn wheat has been found, for example, in the prehistoric settlement of Mureybit of the northern Levantine Corridor dated about 10,000 BP (Renfrew 1973; Fig. 18.1). Then, the mutation that resulted in a non-brittle rachis led to the domestication of einkorn wheat. Using amplified fragment length polymorphism (AFLP) DNA fingerprinting, Heun et al. (1997) located the site of einkorn domestication to the Karacadag region of southeastern Turkey in the northern Levantine Corridor. From here, wild and domesticated einkorn were grown side by side throughout the Fertile Crescent with the non-brittle rachis type gradually replacing wild einkorn. Cultivation of domesticated einkorn then spread to other parts of the Middle East and southern Europe, and eventually central and western Europe (Feldman 2001). Today, einkorn wheat is a relic crop that is grown somewhat in parts of Turkey, Italy, and the former Yugoslavia primarily for animal feed.

18.3.2 Domestication of Emmer Wheat

Wild emmer (*T. turgidum* ssp. *dicoccoides*) is the only true wild polyploid wheat of the lineage, and it is the progenitor of today's durum and bread wheat cultivars. Therefore, the discovery of wild emmer and documentation of its distribution (Aaronsohn 1910) contributed substantially to our understanding of the events that led to the domestication of modern wheats. Unlike wild einkorn wheat, wild emmer does not grow as a weed but only as a truly wild plant mostly confined to relatively undisturbed habitats. Therefore, wild einkorn grows over a much wider area than wild emmer, and the latter has not spread much outside of the Fertile Crescent growing in a region extending from the southern Levant across Israel and Lebanon to southeastern Turkey and across northern Iraq and northwestern Iran (Fig. 18.1). However, the region of wild emmer habitat is not continuous and can be divided into northern and southern subpopulations.

As with einkorn wheat, wild emmer wheat was cultivated for some time before mutants with a non-brittle rachis appeared. Then, wild emmer was likely cultivated for several hundred more years as a mixture with the non-brittle rachis form known as domesticated emmer (*T. turgidum* ssp. *dicoccum*) (Kislev 1984). The archaeological record indicates that, as with domesticated einkorn wheat, domesticated emmer first appeared in the southern Levant and in southeastern Turkey about 9,500–9,000 BP (Nesbitt and Samuel 1996), but the question of where emmer was first domesticated has been debatable. The fact that domesticated emmer showed up in both the northern and southern Levant almost simultaneously suggests that emmer was domesticated in either the northern or southern part and then rapidly spread to the other. Using AFLP analysis, Ozkan et al. (2002) showed that domesticated emmer was more closely related to the northern wild emmer populations than to the southern populations. On the contrary, Mori et al. (2003) evaluated chloroplast microsatellite variation in a more complete set of wild emmer accessions and concluded that emmer was domesticated in the Kartal Dagi mountains of southeastern Turkey, but also suggested emmer may have been domesticated a second time elsewhere. Using the accessions of Mori et al. (2003), Ozkan et al. (2005) conducted AFLP analysis and showed that the Kartal Dagi region was not the site of emmer domestication, and instead suggested that emmer was domesticated in the Karacadag region, the Sulaimaniya region, or both regions independently. Luo et al. (2007) used RFLP fingerprinting to show that emmer was unlikely domesticated in the Sulaimaniya region, but was likely domesticated in the Karacadag region. Substantial gene flow between the northern domesticated emmer population and the southern wild emmer population resulted in high levels of diversity in the southern Levant and led to the development of northern and southern subpopulations of domesticated emmer (Luo et al. 2007). Therefore, both einkorn and emmer were most likely of monophyletic origin and both were domesticated in essentially the same place.

Free-threshing derivatives of domesticated emmer, such as the extinct tetraploid *T. turgidum* ssp. *parvicoccum*, appear in the archaeological record shortly after domesticated emmer (Kislev 1980). In spite of being non-free-threshing, domesticated emmer was the most abundant wheat crop in the Middle East during the Prepottery Neolithic B period, and continued to be a major crop for several thousand years. About 8,000 BP it spread from the northern Fertile Crescent, presumably along with *T. turgidum* ssp. *parvicoccum*, south to Mesopotamia and west to Anatolia, the Mediterranean basin, and Europe (Feldman 2001). It arrived in Egypt, central Asia, and India about 6,000 BP and was the dominant cereal crop in all these regions up until about 3,000 BP when it was largely replaced by free-threshing durum wheat. Today, domesticated emmer is a relic crop grown only in limited areas of the Middle East and south Asia.

18.4 Origin of Free-threshing Tetraploid Wheats

The archaeological record indicates that free-threshing tetraploid wheats appeared about 8,000–9,000 BP in the Prepottery Neolithic B period, about the same time as domesticated emmer. These early finds occurred in Tell Aswad and other Syrian

sites as well as Can Hassan III in southern Turkey (Kislev 1980). This free-threshing tetraploid with very small grains and compact spikes was considered to be an extinct subspecies and given the name *T. turgidum* ssp. *parvicoccum*. It was assumed that this wheat was derived from domesticated emmer (*T. turgidum* ssp. *dicoccum*) and that domesticated emmer was grown for some time before ssp. *parvicoccum* appeared (Feldman 2001). Ssp. *parvicoccum* may have been grown as an admixture with domesticated emmer wheat, or it may have been grown as a separate crop. In either case, it spread along with domesticated emmer throughout the Fertile Crescent and was grown for several millennia in the Middle East. However, some have questioned the existence of ssp. *parvicoccum* due to a limited number of completely characterized samples (Nesbitt 2001).

Durum wheat (*T. turgidum* ssp. *durum*) evolved from domesticated emmer wheat possibly by way of ssp. *parvicoccum*. The first durum wheat was found at Can Hassan III and dated about 6,500–7,500 years BP (Hillman 1978), but durum wheat was not established as a prominent crop until about 2,300 years BP (Feldman 2001). Today, durum is a major crop well adapted to dry climates and used for macaroni and semolina products. It is primarily grown in the Great Plains region of the U.S. and Canada, Russia, India, Italy, and the Middle East.

Most other tetraploid wheat subspecies are free-threshing and probably arose relatively recently. These include spp. *turgidum*, *turanicum*, *polonicum*, *carthlicum*, and others all of which are quite similar to ssp. *durum* and differ by only a few traits. Some, for example ssp. *carthlicum*, probably arose by hybridization between the free-threshing hexaploid *T. aestivum* and another tetraploid (Kuckuck 1979).

18.5 Origin of Hexaploid Wheat

Both free-threshing and non free-threshing forms of cultivated hexaploid wheat exist, but wild progenitors of cultivated hexaploid wheat do not. Hexaploid wheat originated as a result of hybridization between an AB genome-containing tetraploid and the diploid goat grass *Ae. tauschii*, which contributed the D genome (Kihara 1944; McFadden and Sears 1946). A number of studies have pointed to *Ae. tauschii* ssp. *strangulata* as being the donor of the D genome as opposed to ssp. *tauschii* (Nishikawa 1974; Nishikawa et al. 1980; Jaaska 1978, 1980, 1981; Dvorak et al. 1998). *Ae. tauschii* ssp. *strangulata* is distributed in two regions: Transcaucasia and an area of Iran southeast of the Caspian Sea (Fig. 18.1). Therefore, it was thought that the hybridization event that formed hexaploid wheat must have occurred in one of these two areas and several lines of research involving the evaluation of collections of *Ae. tauschii* populations pointed to the area of Iran southeast of the Caspian Sea as the most probable birthplace of hexaploid wheat (Jaaska 1980; Nakai 1979; Dvorak et al. 1998), which most likely involved multiple amphiploidization events between *T. turgidum* and *Ae. tauschii* with subsequent intercrossing that led to the formation of a single gene pool (Dvorak et al. 1998; Lelley et al. 2000).

Because *T. turgidum* was largely confined to the Fertile Crescent and the distribution of *Ae. tauschii* primarily occupies northern Iran, Transcaucasia, and Afghanistan, the hybridization event(s) that resulted in hexaploid wheat probably did not occur until expansion of domesticated emmer subpopulations in the northern Levant overlapped with the primary distribution areas of *Ae. tauschii* in Transcaucasia and south of the Caspian Sea thereby providing the birthplace of hexaploid wheat. However, the South Caspian being the birthplace of hexaploid wheat does not agree with the archaeological record (Nesbitt and Samuel 1996), because the earliest records of hexaploid wheat date to 8,800 to 8,400 BP identified from several areas including Can Hassan III in southern Turkey and Abu Hureyra in Syria (Hillman 1978; Moore et al. 2000; de Moulins 2000; Fairbairn et al. 2002; Fig. 18.1). In line with this, Giles and Brown (2006) reported finding ancient *Ae. tauschii* populations in Syria and Turkey, and obtained results suggesting that the first hybridization event between *T. turgidum* and *Ae. tauschii* that gave rise to hexaploid wheat could have occurred in southeastern Turkey or northern Syria, within the Fertile Crescent near the first archaeological findings. Therefore, while most studies agree that hexaploid wheat is of polyphyletic origin involving more that one *Ae. tauschii*, the exact site of the origin of hexaploid wheat is yet uncertain.

The *T. turgidum* parent involved in the formation of hexaploid wheat is also yet a matter of debate. It is generally accepted that ssp. *dicoccoides* was not the AB-genome donor because, if it were, the resulting hexaploid would have a brittle rachis, and therefore little chance of being selected by farmers (Kimber and Sears 1987). The most probable tetraploid progenitors to hexaploid wheat are domesticated emmer (ssp. *dicoccum*) or an extinct free-threshing subspecies such as ssp. *parvicoccum*, which appear about the same time in the archaeological record. It is interesting to note that Kerber (1964) extracted the AB genome components from hexaploid wheat, and the resulting AB-tetraploids were very similar in spike morphology to ssp. *parvicoccum*. However, some genetic evidence based on genes for waxiness points to domesticated emmer as the AB progenitor (Tsunewaki 1966), while other research based on meiotic restitution suggests free-threshing durum wheat (*T. turgidum* ssp. *durum*) could have been involved (Matsuoka and Nasuda 2004).

Regardless of the subspecies involved, it is certain that *T. turgidum* was the donor of the AB genomes and *Ae. tauschii* donated the D genome to hexaploid wheat (McFadden and Sears 1946). The first hexaploid had hulled seed due to the *Tg1* (tenacious glume; see below) gene acquired from *Ae. tauschii*, and therefore would have been very similar to *T. aestivum* ssp. *spelta* (McFadden and Sears 1946; Kerber and Rowland 1974). Today, two forms of *T. aestivum* ssp. *spelta* exist and are classified as European and Asian spelta. European spelta first appeared in Europe in the Early Bronze Age (4200–3500 BP) near the Swiss lake district and elsewhere (Nesbitt 2001) several thousand years after the appearance of free-threshing hexaploid wheat. It was once thought that European spelta could have been the progenitor to free-threshing hexaploid wheat, but it is now known that it arose more recently as a result of hybridization between *T. aestivum* ssp. *compactum* and domesticated emmer (*T. turgidum* ssp. *dicoccum*) (Bertsch 1943; MacKey 1966; Blatter et al. 2002, 2004; Yan et al. 2003).

Kuckuck (1959) found a spelta-like form of wheat growing in north Iran, and other populations of this Asian spelta are now known to grow in Afghanistan, Tadshikistan, Armenia, and other areas of the Middle East region. Genetic studies have indicated that Asian and European spelta have separate origins (MacKey 1966; Liu and Tsunewaki 1991; Luo et al. 2000), leaving open the possibility that Asian spelta could be the primitive form of common wheat. However, there is no reliable archaeological evidence for the existence of spelta in the regions where hexaploid wheat is thought to have originated, and it is fairly certain that cultivation of free-threshing common wheat preceded the cultivation of hulled hexaploid wheat making it unlikely that Asian spelta is ancestral to common wheat and more likely that it, like European spelta, is a secondary derivative of common wheat.

Neither genetic nor archaeological evidence provide answers as to when and where either type of spelta originated, but it is clear that the first hexaploid must have been spelta-like (McFadden and Sears 1946; Kerber and Rowland 1974). The archaeological record would suggest that neither is ancestral to common wheat, and genetic analysis further rules out European spelta as a primitive form. Therefore, the first hulled hexaploid may have been short-lived and now extinct. This would suggest that the transition from hulled to free-threshing wheat occurred very rapidly, and was probably the result of a mutation of *Tg1* to *tg1* (see below).

The earliest findings of free-threshing ssp. *aestivum* are from Can Hassan III about 8,500 BP, which agrees fairly well with the genetic evidence for the origin of hexaploid wheat occurring about 8,000 BP (Huang et al. 2002). Later finds were unearthed in western Iran, northern Iraq, and western Anatolia followed by finds in the Mediterranean basin and Mesopotamia. Free-threshing common wheat then spread from these areas about 6,000 BP to the Nile Basin, central and western Europe, and Asia.

18.6 Genetics of Domestication Loci

Transitions in three major genes during wheat evolution ultimately yielded free-threshing fully domesticated bread wheat. Those three major genes are *Br*, *Tg*, and *q*, which, in their primitive form, confer a brittle rachis, tenacious glume, and the non free-threshing character, respectively. Mutations in the *Br1* loci on chromosomes 3A and 3B, *Tg1* on 2D, and *q* on 5A had the most profound impacts on domestication characters (Fig. 18.3), but homoeologous copies of each of these genes, and in some cases alternate genetic loci, have also been shown to govern and/or influence domestication traits. Therefore, a relatively detailed synopsis of our understanding of these three major genes, their homoeologs, and other relevant loci is provided below.

18.6.1 Brittle Rachis

A mechanism of natural seed dispersal is a hallmark trait of a wild plant species because it is essential to ensure the spread and propagation of the species. As essential as it is to wild plants, it is as detrimental to cultivated plant species because the fruits or seeds fall to the ground at maturity and are lost. Therefore, the loss of the ability to naturally disperse seed, i.e. the change from a brittle rachis to a non-brittle rachis, was one of the first and most essential domestication traits acquired by the cultivated wheat forms. Seed dispersal systems depend on the formation of abscission zones at particular sites that allow breakage and subsequent dispersal of fruits or seeds. The two basic types of disarticulation found in wheat are spike type, where breakage occurs at the base of the spike and the whole spike is dispersed as a single unit, and spikelet-type, which is further classified into either barrel- (B) or wedge-shaped (W) disarticulation, depending on the disarticulation products. Abscission at the bottom of the spikelet base leaving an adjacent rachis fragment attached behind the spikelet is considered B-type disarticulation. W-type disarticulation is when abscission occurs such that a rachis fragment is left attached below each spikelet.

Wild einkorn wheat (*T. monococcum* ssp. *aegilopoides*) undergoes W-type disarticulation whereas domesticated einkorn, *T. monococcum* ssp. *monococcum* has a non-brittle rachis. Sharma and Waines (1980) showed that non-brittleness in ssp. *monococcum* was controlled by two complementary recessive genes. To my knowledge, the chromosomal locations of these genes have not been determined and therefore their relationships with the other more characterized brittle rachis genes in wheat (see below) are unknown. While the rachis of ssp. *monococcum* is not as fragile as that of ssp. *aegilopoides*, it is not very tough, and moderate pressure causes breakage of the rachis leading to spikelet segments resembling those of wild einkorn. Consequently, the threshing of both forms leads to hulled grains in the form of spikelets with W-type disarticulation. Therefore, the domestication of einkorn wheat may be considered incomplete, or partial, because it involved only one or a few of the several important steps needed toward complete domestication.

Similar transitions occurred in the domestication of cultivated emmer (*T. turgidum* ssp. *dicoccum*) from wild emmer (*T. turgidum* ssp. *dicoccoides*). Studies using genetic stocks where individual pairs of wild emmer chromosomes were substituted for homologous pairs of durum chromosomes have shown that wild emmer chromosomes 3A and 3B harbor genes conferring the brittle rachis trait (Watanabe and Ikebata 2000). Molecular mapping analysis using recombinant inbred chromosome lines derived from the same stocks evaluated by Watanabe and Ikebata (2000) indicated that the *Br* genes are located on the short arms of chromosomes 3A ($Br1^{3A}$) and 3B ($Br1^{3B}$) and that they are likely homoeologous (Nalam et al. 2006; Table 18.1). Both genes lead to W-type disarticulation (Fig. 18.3). This and other studies have also indicated that the *Br1* loci in tetraploid wheat are homoeologous with the *Btr1/Btr2* loci, which confer a brittle rachis in barley (Nalam et al. 2006; Li and Gill 2006). These studies indicate that $Br1^{3A}$ was derived from *T. urartu* and $Br1^{3B}$ from the B-genome donor, and that mutations at both loci were needed to confer the non-brittle

rachis of domesticated emmer. However, like domesticated einkorn wheat, domesticated emmer does not have a very tough rachis and disarticulation is similar to wild emmer when sufficient pressure is applied. Therefore, threshing leads to hulled seed in the form of spikelets for both wild and domesticated emmer (Fig. 18.3).

At least two studies regarding the genetics and mapping of rachis brittleness in wild emmer have reported a *Br* gene on the long arm of chromosome 2A (Peng et al. 2003; Peleg et al. 2011; Table 18.1). While neither study reported the type of disarticulation conferred by the 2A locus, this would suggest that the genetic system involved in controlling spikelet disarticulation is under complex regulation or perhaps the 2A locus represents an independent genetic pathway.

The mutations in the wild emmer *Br* loci happened before the amphiploidization event that gave rise to hexaploid wheat. Therefore, with the exception of *T. aestivum* ssp. *macha* (which was likely formed secondarily) none of the hexaploid subspecies have the primitive $Br1^{3A}$ or $Br1^{3B}$ alleles and therefore do not have brittle rachises conferred by these genes. A hexaploid semi-wild wheat landrace was found in Tibet and reported to have a fragile rachis and W-type disarticulation (Cao et al. 1997). It was later determined that rachis brittleness in this line was due to a *Br* gene ($Br1^{3D}$) on the short arm of 3D, which was likely derived from *Ae. tauschii* and homoeologous to $Br1^{3A}$ and $Br1^{3B}$ (Chen et al. 1998; Table 18.1). However, *Ae. tauschii* has B-type disarticulation and so it was suggested that $Br1^{3D}$ likely confers B-type disarticulation in *Ae. tauschii* but W-type in a hexaploid background. Further work by Li and Gill (2006) indicated that B-type disarticulation in *Ae. tauschii* is conferred by a *Br* gene ($Br2^{3D}$) on the long arm of chromosome 3D. They concluded that B- and W-type disarticulations are controlled by different genes with $Br1^{3A}$, $Br1^{3B}$, and $Br1^{3D}$ controlling W-type and $Br2^{3D}$ controlling B-type. In either case, the *Br* gene(s) present in the *Ae. tauschii* progenitor must have undergone mutation very soon after the hybridization event that gave rise to hexaploid wheat, or if the *Ae. tauschii* progenitor carried only $Br2^{3D}$, its effects are greatly diminished in a hexaploid background.

18.6.2 Tenacious Glume

The primitive non-domesticated wheat forms had tough glumes that tightly enveloped the seed in order to protect it during natural seed dispersal. Domesticated einkorn wheat, the only cultivated diploid wheat, is not free-threshing because it has tough adherent glumes that do not allow the seed to be easily separated from the spikelets. Investigation of a spontaneous free-threshing mutant of domesticated einkorn wheat, referred to as *T. sinskajae*, indicated that a single recessive gene designated *sog* controlled the soft glume trait and mapped to the short arm of chromosome $2A^m$ (Taenzler et al. 2002; Sood et al. 2009).

The glumes of wild and domesticated emmer are tough, hold the kernels tightly, and prohibit the free-threshing trait (Fig. 18.3). Simonetti et al. (1999) evaluated a tetraploid mapping population derived from a cross between *T. turgidum* spp.

Table 18.1 The three principal traits affected by mutation leading to wheat domestication and their associated genetic loci

Trait	Gene	Chrom. arm	Species that acquired mutation to domestic form (ploidy)	Reference
Brittle rachis	$Br1^{3A}$	3AS	*T. turgidum* ssp. *dicoccum* (4 ×)	Watanabe and Ikebata (2000) Nalam et al. (2006) Li und Gill (2006)
	$Br1^{3B}$	3BS	*T. turgidum* ssp. *dicoccum* (4 ×)	Watanabe and Ikebata (2000) Nalam et al. (2006) Li und Gill (2006)
	$Br1^{3D}$	3DS	*T. aestivum* ssp. *aestivum* (6 ×)	Chen et al. (1998)
	$Br2^{3D}$	3DL	*T. aestivum* ssp. *aestivum* (6 ×)	Li und Gill (2006)
	$Br4^{2A}$	2AL	*T. turgidum* ssp. *dicoccum* (4 ×)	Peng et al. (2003, 2011)
Tenacious glume	$Tg1^{2D}$	2DS	*T. aestivum* ssp. *aestivum* (6 ×)	Jantasuriyarat et al. (2004) Nalam et al. (2007) Sood et al. (2009)
	$Tg2^{2B}$	2BS	*T. turgidum* ssp. *parvicoccum* (4 ×)[a]	Simonetti et al. (1999)
Free-threshing	Q^{5A}	5AL	*T. turgidum* ssp. *parvicoccum* (4 ×)[a] or *T. aestivum* ssp. *aestivum* (6 ×)	Faris et al. (2005) Simons et al. (2006)

[a] This subspecies is not known for certain and could have been *parvicoccum*, *durum*, or perhaps another tetraploid subspecies

dicoccoides and *durum* for quantitative trait loci (QTLs) associated with the free-threshing trait. One QTL corresponded to the free-threshing locus *Q* on the long arm of chromosome 5A (see below) and another with major effects mapped to the short arm of chromosome 2B. The latter QTL was located in a position apparently syntenic with the tough glume gene $Tg1^{2D}$ on chromosome 2D (see below). It is possible that the gene underlying the 2B QTL ($Tg2^{2B}$) and $Tg1^{2D}$ (Table 18.1) are homoeologous, or that $Tg2^{2B}$ is homoeologus with *Sog* on $2A^m$ in einkorn wheat, but appropriate comparative mapping experiments to address these matters have not been conducted. Another matter to be addressed is whether or not domesticated emmer (*T. turgidum* ssp. *dicoccum*) possesses $Tg2^{2B}$, or if the tough glume, non-free-threshing trait of domesticated emmer is due to the fact it carries the *q* allele on 5A. The finding that *T. turgidum* ssp. *dicoccum* var. *liguliforme*—a variety of domesticated emmer with a dense spike—carries the *Q* allele on 5A yet is non-free-threshing due to tough adherent glumes (Muramatsu 1979; Simons et al. 2006) would suggest that domesticated emmer probably carries the $Tg2^{2B}$ allele. No *Tg* gene has been

described on the A genome of polyploid wheat or from the A-genome progenitor *T. urartu*.

Kerber and Dyck (1969) first described the tenacious glume trait in wheat and attributed the character to an incompletely dominant gene $Tg1^{2D}$. Early cytogenetic work placed $Tg1^{2D}$ on the short arm of chromosome 2D (Kerber and Rowland 1974), and more recent molecular mapping experiments have validated the position of $Tg1^{2D}$ on chromosome arm 2DS (Jantasuriyarat et al. 2004; Nalam et al. 2007; Sood et al. 2009; Table 18.1). Sood et al. (2009) demonstrated that $Tg1^{2D}$ and *sog* are not homoeologous suggesting that $tg1^{2D}$ and *Sog* arose from independent mutations at non-orthologous loci. Therefore, it is possible that $Tg2^{2B}$ is homoeologous with either *Sog* on $2A^m$ from einkorn wheat or $Tg1^{2D}$, but not both. Additional analysis by Nalam et al. (2007) suggested that two closely linked, possibly paralogous, $Tg1^{2D}$ loci exist on 2DS. Further work is necessary to validate this work and to clarify the genetic relationships among the *Tg/sog* loci.

18.6.3 The Q Loci

In addition to the *Tg* loci, the *Q* locus on wheat chromosome 5A also controls the free-threshing character. A mutation in the primitive q^{5A} allele led to the formation of the partially dominant Q^{5A} allele, which results in free-threshing seed (Fig. 18.3, Table 18.1). *Tg* is epistatic to *Q* because plants that have $Tg1^{2D}$ and Q^{5A} are not free-threshing (Kerber and Rowland 1974), but both the $tg1^{2D}$ and Q^{5A} alleles are necessary to confer the free-threshing trait (Fig. 18.3). The *Q* locus has been an intriguing subject of study for the past 100 years due to the fact that it affects a repertoire of traits. Plants that have *br* and *tg* alleles but lack the Q^{5A} allele (possess the q^{5A} allele) are non-free threshing, have a semi-brittle rachis, a spike that is lax and primitive in appearance (speltoid), somewhat tenacious glumes that adhere to the seed, and are taller, flower earlier, and differ in yield compared to plants that harbor the Q^{5A} allele (Watkins 1940; Mackey 1954, 1966; Sears 1956; Muramatsu 1963, 1979, 1985, 1986; Singh 1969; Kato et al. 1999, 2003; Faris and Gill 2002; Faris et al. 2003, 2005; Simons et al. 2006; Zhang et al. 2011). Therefore, Q^{5A} pleiotropically affects numerous domestication-related and agronomically important traits.

Of the major domestication genes in wheat, *Q* is the only one that has been cloned so far (Faris et al. 2003; Simons et al. 2006). *Q* is a member of the AP2 family of transcription factors. Related members include *APETALA2*, which controls flower and seed development in *Arabidopsis* (Jofuku et al. 1994) and *indeterminate spikelet1* (*ids1*), which governs spikelet meristem fate in maize (Chuck et al. 1998). Homologs also exist in the other grasses such as rice, barley, *Brachypodium*, and sorghum (Simons et al. 2006; Faris et al. 2008), but functions have not been ascribed to the gene in these species. So far, wheat is the only plant species known for which this *AP2*-like gene has been recruited for domestication.

DNA sequence analysis of Q^{5A} and q^{5A} alleles from various wheat species of different ploidy levels validated the notion that q^{5A} is the more primitive allele and

that Q^{5A} formed once as the result of a mutation (Simons et al. 2006). This work also demonstrated that the A-genome diploids *T. monococcum* ssp. *monococcum* and *T. urartu* as well as the AB tetraploids *T. turgidum* spp. *dicoccoides* and *dicoccum*, and hexaploid *T. aestivum* spp. *macha* and *spelta* (European) all possess the primitive q^{5A} alleles. The free-threshing wheats including the tetraploids *T. turgidum* spp. *polonicum*, *carthilicum*, and *durum*, the free-threshing hexaploid *T. aestivum* ssp. *aestivum*, and also the non free-threshing *T. aestivum* ssp. *spelta* (Asian) shown by Luo et al. (2000) to have Q^{5A}, were all verified to have the Q^{5A} allele. The latter finding further supports the notion that Asian spelta has an origin different from that of European spelta and that it probably possesses either $Tg1^{2D}$ or $Tg2^{2B}$, which would mask the effects of the free-threshing Q^{5A} allele.

Comparative sequence analysis revealed only one conserved structural difference between Q^{5A} and q^{5A} alleles at the protein level: all q^{5A} alleles harbored a valine at amino acid position 329 whereas all Q^{5A} alleles had an isoleucine (Simons et al. 2006). The V_{329} to I mutation was found to lead to an abundance of homodimer formation by the Q^{5A} protein. Transcription levels of Q^{5A} were also found to be more than twice the level of q^{5A}, and it is hypothesized that protein homodimerization may be a mechanism of self-regulation. Indeed, increased transcription levels of Q^{5A} and its effects on the domestication-related phenotypes were clearly demonstrated in transgenic plants (Simons et al. 2006), which confirmed the reports of Muramatsu (1963) regarding the dosage effects of *Q* using cytogenetic stocks. Another potential mechanism of *Q* regulation is a microRNA172 binding site in exon 10, which could mimic the regulation of *APETALA2* in *Arabidopsis* at the level of translation.

Clearly more work is needed to understand the mechanisms responsible for *Q* gene regulation, and its interactions with other genes. For example, Jantasuriyarat et al. (2004) evaluated a population of recombinant inbred lines derived from a cross between a hexaploid wheat variety and a synthetic hexaploid wheat line, which was created by crossing *T. turgidum* ssp. *durum* with *Ae. tauschii* followed by chromosome doubling thereby essentially repeating the hybridization event that led to formation of hexaploid wheat (a practice that is routinely done for the exploitation of desirable traits from the progenitor species). QTL analysis of the threshability trait revealed a locus with strong effects on the short arm of chromosome 2D in the vicinity of $Tg1^{2D}$, as was expected because the synthetic parent is non free-threshing due to $Tg1^{2D}$ from the *Ae. tauschii* parent. However, a QTL on 5A near the *Q* locus was also detected, which was unexpected due to the assumption that both parents possessed the Q^{5A} allele. The effects of the Q^{5A} locus were thereby attributed to possible allelic variation within Q^{5A}. Similar work using a population of doubled haploid lines derived from different synthetic and cultivated wheat parents and subsequent analysis of QTL associated with threshability revealed essentially the same results (Faris JD, Chu CG, Friesen TL, Xu SS, unpublished). But, in this case we sequenced the Q^{5A} alleles from both parents and found no variation within the gene coding sequences. This might suggest that the effects of the *Q* locus on threshability in synthetic hexaploid-derived populations could be due to variation in Q^{5A} gene expression, possibly influenced by $Tg1^{2D}$ or other genes. Work is currently underway to gain further understanding of this phenomenon.

Homoeologous *q* loci on chromosomes 5B and 5D were long thought to exist and the work of Simons et al. (2006) proved it so. Zhang et al. (2011) conducted studies to better understand the evolution, organization, and function of homoeologous q^{5B} and q^{5D} alleles and their relationships with Q/q^{5A} alleles. Their analysis revealed that *Q/q* gene sequences were highly conserved among A, B, and D genomes in hexaploid wheat, the A and B genomes in tetraploid wheat, and the A, S, and D genomes in the diploid progenitors, but a duplication of the *q* gene prior to radiation of the diploid progenitors some 5.8 million BP was followed by the selective loss of one copy from the A genome progenitor and the other copy from the B, D, and S genomes. *Ae. tauschii* as well as hexaploid wheat possess intact and functional q^{5D} alleles, and functional and phenotypic analysis indicated that q^{5D} contributes to the suppression of the speltoid syndrome just as Q^{5A}, but to a lesser degree. *Ae. speltoides* possessed an intact and functional q^{5S} allele, but q^{5B} became a pseudogene upon formation of the AB tetraploid. However, q^{5B} still contributes to domestication-related traits through mechanisms of homoeoallele co-regulation in a rather complex manner. Therefore, while the mutation that gave rise to Q^{5A} from q^{5A} was a major factor in domesticating wheat, the contributions of q^{5B} and q^{5D} through polyploidization are also recognized as relevant contributors.

18.6.4 The Evolution of Free-threshing Wheats

A set of rather profound circumstances occurred in the formation of free-threshing polyploid wheat, especially given that the evolutionary steps involved mutations at three major loci (*Br*, *Tg*, and *q*) and two allopolyploidization events. Some of the events and transitions are well understood, while others are not, but clearly both genetics and the archaeological record indicate that all these events happened during an "evolutionary burst" that occurred relatively quickly over a period of less than a few thousand years. The first transition was of course the acquisition of a non-brittle rachis in *T. turgidum*. This required mutations in both $Br1^{3A}$ and $Br1^{3B}$ in wild emmer leading to the formation of domesticated emmer (Figs. 18.2, 18.3). Although domesticated emmer has a non-brittle rachis, it is not free-threshing because it carries the q^{5A} allele and most likely $Tg2^{2B}$ (Fig. 18.2). Free-threshing tetraploid wheat evolved from domesticated emmer by way of the mutation in q^{5A} that gave rise to Q^{5A} and also likely $Tg2^{2B}$ to $tg2^{2B}$ thus forming the free-threshing tetraploid, which is the genotype of today's modern durum wheat. Not only did the mutation to Q^{5A} result in the free-threshing character, it also conferred a fully tough rachis.

It is most likely that a free-threshing tetraploid was involved in the amphiploidization event that gave rise to the first hexaploid (Fig. 18.2). However, the first hexaploid was non free-threshing due to acquisition of the $Tg1^{2D}$ gene from *Ae. tauschii*. It also likely acquired genes from *Ae. tauschii* for brittle rachis, possibly $Br1^{3D}$, $Br2^{3D}$, or both, and had the genotype $br1^{3A}br1^{3A}br1^{3B}br1^{3B}Br1^{3D}Br1^{3D}Br2^{3D}Br2^{3D}tg2^{2B}tg2^{2B}Tg1^{2D}Tg1^{2D}Q^{5A}Q^{5A}q^{5B}q^{5B}q^{5D}q^{5D}$. Therefore, mutations in $Tg1^{2D}$ and *Br* gene(s) obtained from *Ae. tauschii* were necessary in the transition of this

"Asian spelta-like" wheat to modern free-threshing *T. aestivum* ssp. *aestivum*. If the AB genome donor were domesticated emmer, the first hexaploid would have had to undergo mutations in q^{5A} and probably $Tg2^{2B}$ in addition to $Tg1^{2D}$ and possibly $Br1^{3D}$ and/or $Br2^{3D}$ to give rise to *T. aestivum* ssp. *aestivum*. Under this unlikely scenario, the free threshing tetraploids would have evolved later than free-threshing hexaploids through the acquisition of Q^{5A} from *T. aestivum* ssp. *aestivum*.

The archaeological record does not shed much light on the unknowns of these scenarios. Free-threshing tetraploids and hexaploids appear at the same time, shortly after the appearance of domesticated emmer, so the exact AB tetraploid progenitor and the answer to whether Q^{5A} first arose in the tetraploids or the hexaploids is yet unknown. Also, no primitive non free-threshing hexaploids precede the free-threshing hexaploids in the archaeological record. Genetic studies have discovered the origin of European spelta, and indicate that it is a derivative rather than a progenitor of *T. aestivum* ssp. *aestivum*, but no genetic evidence allows conclusions on whether or not Asian spelta is an ancient wheat or the result of a recent hybridization.

If the hybridization event that gave rise to hexaploid wheat occurred when *Ae. tauschii* came into contact with a field of free-threshing tetraploid wheat, the result would have been a hulled hexaploid growing in a field of free-threshing tetraploid wheat. As Nesbitt (2001) points out, early farmers would have processed hulled wheats different from free-threshing wheats, and as a result, hulled wheat grown in a free-threshing field would have been under strong selection pressure to become free-threshing itself. Thus, the transition would have occurred rapidly, which would explain large absence of spelt wheat from the Middle East. If domesticated emmer hybridized with *Ae. tauschii* to form the first hexaploid, mutations would have had to occur at q^{5A}, two *Tg* loci, and possibly two *Br* loci at the same time to explain the absence of spelt from the archaeological record. And, under this unlikely scenario, a free-threshing tetraploid would not have yet existed because we know that the mutation forming Q^{5A} occurred only once, indicating that Q^{5A} (and possibly $tg2^{2B}$) would have been acquired by an AB-tetraploid via gene flow from the hexaploid. This gene-flow event would have had to occur very rapidly to explain the appearance of free-threshing tetraploids and hexaploids at the same time. Whatever the scenario, the transitions necessary for free-threshing tetraploid and hexaploid wheat to evolve must have occurred very rapidly. Cloning and further genetic analysis of *Tg* and *Br* loci along with *Q/q* genes should provide more definitive answers to these unknowns in the future.

18.7 Wheat Evolution Under Cultivation

18.7.1 Capture of Genetic Variability

Domesticated emmer wheat arose through very few mutations in their wild progenitor subspecies, making the first domesticated form genetically very similar to the corresponding wild form. Even though domesticated emmer is by and large a

self-pollinated species, hybrids between wild and domesticated tetraploids are fully fertile and their chromosomes readily pair and recombine. Early farmers grew domesticated emmer in mixtures with wild emmer for a long period of time allowing ample opportunity for gene flow to occur leading to increased genetic variability, formation of sub-populations, and reduction of the founder effect (Luo et al. 2007). Gene flow has continued to occur even after domesticated emmer largely replaced wild emmer and other tetraploid wheats have come to exist such as today's economically important durum wheat. Many of the subspecies come into contact with each other at the edges of fields of cultivated durum or even hexaploid wheat and form hybrid swarms resulting in gene flow from wild to cultivated forms and vice versa (Dvorak et al. 2006; Syouf et al. 2006).

The founder effect for hexaploid wheat is much larger compared to emmer wheat because very few hybridization events between *T. turgidum* and *Ae. tauschii* occurred resulting in a larger magnitude of genetic drift. This and the fact that hexaploid was relatively isolated genetically because it hybridizes less frequently with its progenitors resulted in a much narrower genetic base and reduced variability compared to domesticated tetraploid wheats. However, the level of diversity is less restricted in the A and B genomes compared to the D genome, and in support of this, studies have shown that hybrid swarms involving wild emmer and common wheat exist and that gene flow from the former to the latter has occurred (Dvorak et al. 2006). In line with this, there is strong evidence that the hexaploid *T. aestivum* spp. *macha* and *spelta* (European), which have primitive traits, originated from interspecific crosses involving hexaploids and tetraploids (Bertsch 1943; MacKey 1966; Dvorak and Luo 2001; Blatter et al. 2002, 2004; Yan et al. 2003), and the tetraploid *T. turgidum* ssp. *carthlicum* probably arose through gene flow involving hexaploid wheat (Kuckuck 1979). Therefore, these new subspecies may have resulted from hybrid swarms as well.

18.7.2 Further Domestication Under Cultivation

Increased seed size was also an important domestication trait, and was selected for very early in the first years of wheat cultivation, probably before the acquisition of a non-brittle rachis (Fuller 2007). Seed size is under polygenic control and genes and QTLs governing this trait have been located on many wheat chromosomes (Peng et al. 2011). Following the transition to a non-brittle rachis, other traits acquired by newly domesticated emmer wheat included non-dormant seeds with uniform germination, yield, and probably more erect plants (Feldman 2001). As with seed size, many of these traits are under polygenic control and multiple QTLs associated with these traits have been reported (Peng et al. 2003, 2011). The spread of wheat cultivation throughout Europe, Africa, and Asia also required wide adaptation to the different environments, which included alterations in flowering time and growth habit.

According to Feldman (2001), a second phase of evolution under cultivation involved a lengthy period of time where continuous selection occurred for various

traits in fields consisting of mixtures of different genotypes and likely even different species of different ploidy levels. These mixtures of different landraces provided some protection against disease epidemics and probably some environmental hazards such as drought, extreme heat, and flooding as well. Therefore, the cultivation of these mixtures provided some level of crop security and ensured yield stability. These mixtures also provided ample opportunity for interspecific hybridizations and gene flow, thus increasing genetic variability. However, they also created a competitive environment where plants that had more tillers and were taller with horizontal leaves would shade the competitors and thus have a selective advantage.

The dawn of modern breeding practices began about a century ago. Since that time, individual genotypes have been the unit of selection rather than mixtures, which has led to wheat fields consisting of single genotypes with no opportunity for interspecific genetic exchange to increase variability. However, plant breeding practices in the mid-20th century allowed the development of the first uniform high-yielding cultivars through the introgression of elite agronomic characters. A profound example of this was the replacement of tall varieties with semi-dwarf and dwarf varieties though the introduction of the *Rht* genes. This occurred during the "green revolution" under the leadership of Norman E. Borlaug at the International Maize and Wheat Improvement Centre (CIMMYT) in Mexico. Breeding practices today allow extensive and intricate manipulations of the wheat plant to be made with certainty as well as rather precise monitoring of introgressions and genetic exchanges resulting from artificial hybridizations through the use of modern genomics tools and resources.

18.7.3 Generation of New Genetic Diversity

Although hexaploid wheat captured a good amount of genetic diversity for the A and B genomes, the genetic bottlenecks created by domestication resulted in the increased frequency of many adapted alleles but also the loss of other potentially useful ones. This limited amount of diversity reduces the potential for wheat to further adapt to changing environments. However, genomic analyses of wheat and its relatives over the past decade has revealed the wheat genomes in a polyploid state are dynamic and undergo the generation of new variation in the form of deletions, insertions, and point mutations created by repetitive elements affecting genes and regulatory elements (Dubcovsky and Dvorak 2007). Such alterations are well tolerated in wheat due to its polyploid buffering capacity. These alterations in gene coding regions create intergenic polymorphisms, which further increases genetic variability among the genomes and may lead to subtle changes in expression due to gene dosage differences. Alternatively, homoeologous sets of genes in a polyploid state are given the opportunity to become altered, for example, through sub-functionalization (becoming limited in function) or neo-functionalization (acquiring a new function). A good example of this is *Q* and its homoeoalleles because under polyploidization, Q^{5A} became hyper-functional, q^{5B} underwent pseudogenization, and q^{5D} became

sub-functionalized (Zhang et al. 2011). Therefore, to some extent, polyploid wheat is able to create a level of its own diversity due to the plasticity of its genomes and cooperation between genetic mutations created by repetitive elements and tolerance through polyploid buffering. Nevertheless, we need to make concentrated efforts to preserve a large reservoir of wild relatives and landraces through germplasm collections and gene banks so that we have the ability to introduce additional variability when needed.

18.8 Future Needs

Today's wheat varieties are far superior in yield, quality, biotic and abiotic resistance, and overall agronomic performance then even those that were considered elite just a few decades ago. However, more profound advances in these and other traits must be made in the near future if we are to feed the world's growing population. Significant advances in our understanding of the biology of the wheat plant must be achieved, and this can be initiated through the cracking of the genetic code of wheat and characterizing the structure and function of critical genes (see chapter by C. Feuillet). Obtaining the genome sequence of polyploid wheat and its relatives will also allow scientists to conduct studies that yield important information that may help answer unknowns regarding wheat evolution and domestication. This in turn will help wheat scientists to better cope with global climate change by allowing the recovery and exploitation of valuable alleles that exist in key wheat relatives. Under a continuously changing climate, the world may well see a need for another agricultural revolution and neo-domestication of wheat in order to meet future demands.

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