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Domestication and crop evolution of wheat and barley: Genes, genomics, and future directions[FA]

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Invited Expert Review

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Abstract Wheat and barley are two of the founder crops of the agricultural revolution that took place 10,000 years ago in the Fertile Crescent and both crops remain among the world's most important crops. Domestication of these crops from their wild ancestors required the evolution of traits useful to humans, rather than survival in their natural environment. Of these traits, grain retention and threshability, yield improvement, changes to photoperiod sensitivity and nutritional value are most pronounced between wild and domesticated forms. Knowledge about the geographical origins of these crops and the genes responsible for domestication traits largely pre-dates the era of next-generation sequencing, although sequencing will lead to new insights. Molecular markers were initially used to calculate distance (relatedness), genetic diversity and to generate genetic maps which were useful in cloning major domestication genes. Both crops are characterized by large, complex genomes which were long thought to be beyond the scope of whole-genome sequencing. However, advances in sequencing technologies have improved the state of genomic resources for both wheat and barley. The availability of reference genomes for wheat and some of its progenitors, as well as for barley, sets the stage for answering unresolved questions in domestication genomics of wheat and barley.

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INTRODUCTION

Wheat and barley are two of the founding crops that started the agricultural revolution about 10,000 years ago in the Fertile Crescent (Zohary et al. 2012). In fact, many of the wild progenitors of these crops still exist in this region (Harlan and Zohary 1966). Cultivated barley (*Hordeum vulgare* L. ssp. *vulgare*) is remarkably morphologically similar to its wild progenitor, *Hordeum vulgare* ssp. *spontaneum*; hereafter *H. spontaneum* for short (Figure 1). However, the domestication history for wheat is more complex. Hexaploid bread wheat (*Triticum aestivum* L. ssp. *aestivum*) derives its three genomes (A, B and D) from three diploid wild ancestors: *Triticum urartu* Tumanian ex Gandylian, an unknown relative of *Aegilops speltoides* Tausch and *Ae. tauschii* Coss, respectively. These three ancestors, and other grasses within the Triticeae, are related to one another by descent and through ancestral hybridization (Marcussen et al. 2014). Further, each of the ancestors has apparently undergone ancient polyploidization events, followed by subsequent

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Figure 1. A graphical representation of barley evolution and domestication
Wild barley is shown on the left, two-rowed domesticated barley in the middle and six-rowed domesticated barley on the right. (Artwork credit: Mona Schreiber).

reversion to diploid states (Pont and Salse 2017; Glemin et al. 2018).

The A genome was contributed by *T. urartu* (A^uA^u), although *T. urartu* itself was never domesticated (Dvořák et al. 1993) during an amphiploidization event which took place no more than 0.5 million years ago (Chalupska et al. 2008). During this event, the B genome was contributed by a member of the sitopsis group of *Aegilops* (Blake et al. 1999). The egg donor in this initial hybridization event was the donor of the B genome and the pollen donor contributed the A genome; therefore, the genome formula for tetraploid wheats should be written as BBAA (Özkan et al. 2011), although some other authors choose to write the formula alphabetically as AABB. Consequently, the hexaploid formula should be BBAADD.

The result of the initial hybridization event was tetraploid (emmer) wheat *T. turgidum* ssp. *dicoccoides* (Körn.) Thell (Chalupska et al. 2008). Cultivated tetraploid emmer wheat *T. dicoccum* (syn: *T. dicoccon*) and later, durum wheat (*T. turgidum* ssp. *durum*) arose from this wild ancestor. Cultivated diploid einkorn, *T. monococcum* ssp. *monococcum* (A^mA^m), was derived from *T. monococcum* ssp. *boeoticum* (A^bA^b), a close relative of *T. urartu*. Today, einkorn is considered a relic crop since it has largely been supplanted by agronomically superior wheats (Salamini et al. 2002; Kilian et al. 2007).

About 8,000 years ago, a second hybridization event took place between domesticated emmer wheat and the donor of the D genome, *Ae. tauschii*, giving rise to modern bread wheat (Peng et al. 2011; Wang et al. 2013). It is believed that this event occurred when cultivation of domesticated emmer wheat spread into the natural range of *Ae. tauschii* (Salamini et al. 2002). Another species of domesticated hexaploid wheat, spelt (*T. aestivum* ssp. *spelta*) was widely cultivated in Europe until the 20th century when it was largely replaced by bread wheat due to the agronomic superiority of the latter; however, spelt is still grown to a limited extent in Central Europe, particularly on marginal land, and may provide a valuable resource for future bread wheat improvement (Longin and Würschum 2016; Müller et al. 2018). Figure 2 shows a graphical representation of critical steps in wheat domestication.

The origin of spelt raises some interesting questions about the domestication process. Since spelt is not free-threshing, it can be considered to be more primitive than free-threshing bread wheat, at least from an anthropocentric view. Two genes are important for the free-threshing character: tenacious glumes (*Tg*) and the domestication locus *Q* (which also affects other domestication traits). These genes will be discussed in further detail later in this review.

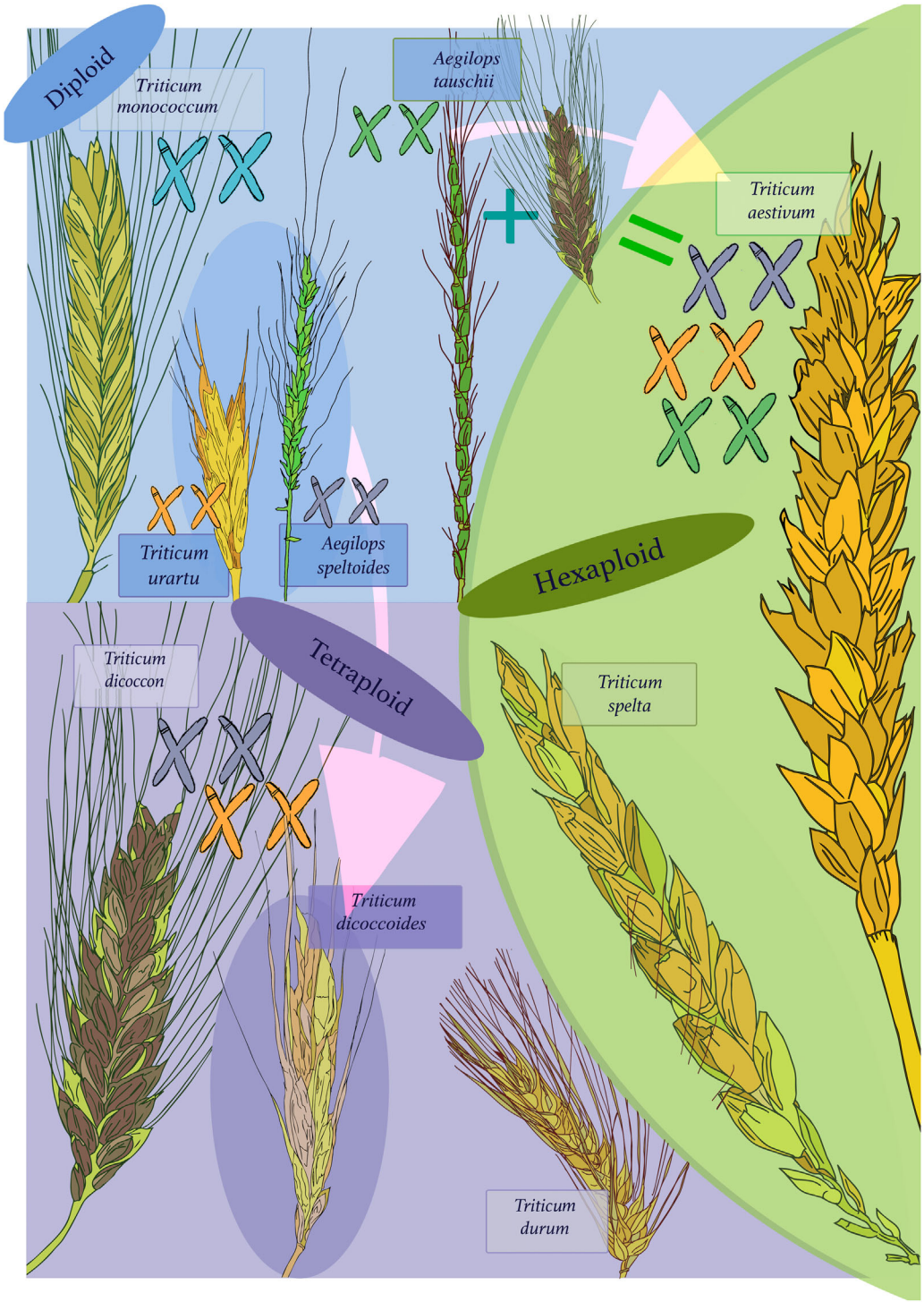

Figure 2. A graphical representation of wheat evolution and domestication
Several diploid ancestors have contributed to the genome of modern wheat. A polyploidization event between a member of the sitopsis group, possibly *Aegilops speltoides* (BB), and *Triticum urartu* (AA) resulted in *Triticum dicoccoides* (wild emmer; BBAA). *Triticum dicoccum* (domesticated emmer; BBAA) and *Triticum durum* (durum; BBAA) are derived from this lineage. Hexaploid *Triticum aestivum* ssp. *aestivum* (bread wheat; BBAADD) arose from a hybridization of domesticated emmer (BBAA) with *Aegilops tauschii* (goat grass; DD). The origin of hexaploid *Triticum aestivum* ssp. *spelta* (spelt; BBAADD) is still controversial, although it is probably not an ancestor to bread wheat, but rather the result of hybridization between bread wheat and an emmer species. (Artwork credit: Mona Schreiber).

It is widely accepted that bread wheat arose from a hybridization event between free-threshing tetraploid emmer wheat (*tg-A1*/*tg-A1; tg-B1*/*tg-B1*; QQ) and *Ae. tauschii* (*Tg-D1*/*Tg-D1*) (Dvorak et al. 2012). In this scenario, early hexaploid would have been hulled due to the tenacious glumes (*Tg-D1*/*Tg-D1*) contributed by *Ae. tauschii*. Thus, spelt may be a direct ancestor of bread wheat; however, the evidence suggests European spelt originated from a secondary hybridization of free-threshing hexaploid wheat with a tetraploid wheat (Blatter et al. 2004). In contrast to European spelt, Asian spelt may represent an intermediate stage between free-threshing tetraploid wheat and free-threshing hexaploid wheat. The presence of *Tg-D1* and *Q* alleles support this hypothesis; however, *Tg-B1* also exists in the Asian spelt gene pool, which contradicts this hypothesis (Dvorak et al. 2012).

Domestication traits

A number of phenotypic differences exist between domesticated and wild species that are mirrored by differences at the genetic level. These differences, including non-dehiscent spikes, free-threshing grain, reduced seed dormancy and altered flowering time are key to domestication because they control traits that facilitate human collection and consumption, which would otherwise be deleterious in nature. These traits may be considered as domestication traits or crop evolution under domestication traits. The difference between the two terms depends on whether there is a clear dimorphism between wild and domesticated plants, such as shattering in cereals, or whether variation exists between both groups.

For some traits which exist only in domesticated genotypes, such as the six-rowed spike (ruling out the feral variety '*agriocrithon*'), the underlying genes should then be considered as crop evolution under domestication genes because the wild type (two-rowed spike) also exists in domesticated genotypes (Abbo et al. 2012; Abbo et al. 2014). A summary of major domestication and crop evolution under domestication genes is provided in Table 1 and graphically depicted in Figure 3. The *Non-brittle rachis* genes control the first and arguably one of the most important of these traits, seed retention, and are conserved across the Triticeae genomes on the short arm of the homoeologous group 3 chromosomes.

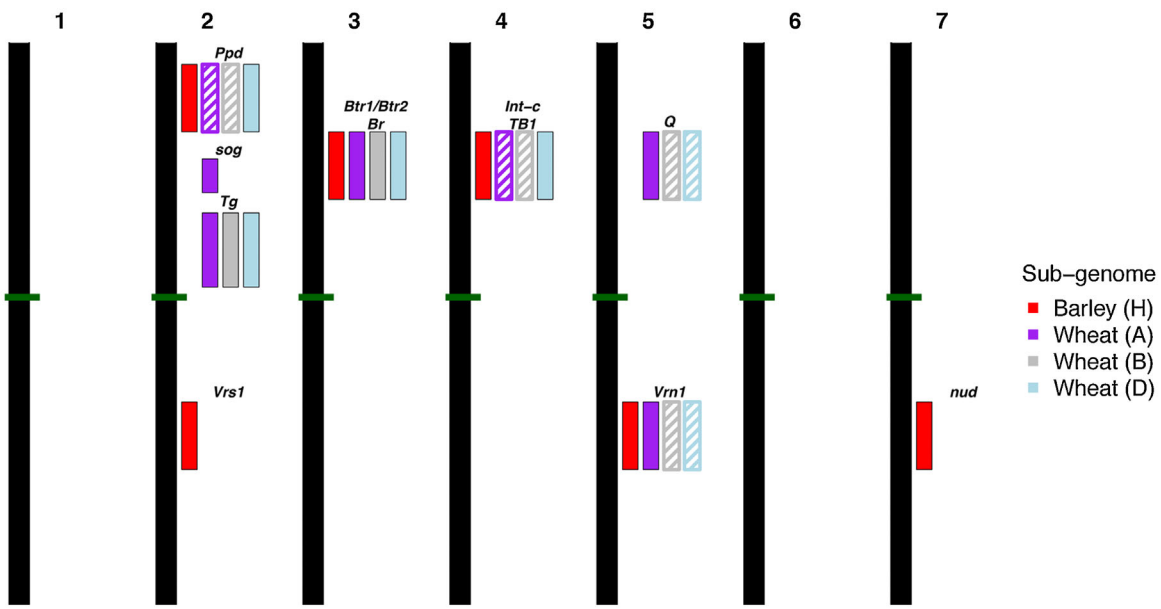

Figure 3. A comparison of important domestication/improvement loci between wheat and barley

Vertical black bars represent individual chromosomes and the centromere of each chromosome is represented by a small, green rectangle. Colored bars represent genome-specific genes. For most cases, homologs exist in all three wheat genomes, but only the most important of the three copies is filled. The others are shown because they are known to exist, but are only partially colored.

Table 1. Key domestication/improvement genes for wheat and barley

Crop	Gene	Gene product	Gene type[a]	Chromosome	Cloned?	Reference(s)
Barley	*thresh-1*	unknown	Crop evolution	1H	No	Schmalenbach et al. 2011
	Ppd-H1	Pseudo-response regulator	Crop evolution	2H	Yes	Turner et al. 2005
	Vrs1	Pseudo-response regulator	Crop evolution	2H	Yes	Komatsuda et al. 2007
	Btr1/Btr2	Cloned, but exact function unknown	Domestication	3H	Yes	Pourkheirandish et al. 2015
	Int-c	Transcription factor (TESOSINTE BRANCHED 1)	Domestication	4H	Yes	Ramsay et al. 2011
	Vrn1	MADS box transcription factor	Crop evolution	5H	Yes	Komatsuda et al. 2007
	nud	Ethylene response factor	Crop evolution	7H	Yes	Taketa et al. 2008
Wheat	*Ppd-A1*	Pseudo-response regulator	Crop evolution	2A	No	Maccaferri et al. 2008
	Ppd-B1	Pseudo-response regulator	Crop evolution	2B	No	Wilhelm et al. 2009
	Ppd-D1	Pseudo-response regulator	Crop evolution	2D	No	Beales et al. 2007
	sog		Crop evolution	2A	No	Taenzler et al. 2002 Sood et al. 2009
	Tg-A1	unknown	Crop evolution	2A	No	
	Tg-B1	unknown	Crop evolution	2B	No	Faris et al. 2014
	Tg-D1	unknown	Crop evolution	2D	No	
	Br-A1 (Br_2)	unknown	Domestication	3A	No	Watanabe et al. 2002
	Br-B1 (Br_3)	unknown	Domestication	3B	No	Watanabe et al. 2002
	Br-D1 (Br_1)	unknown	Domestication	3D	No	Watanabe et al. 2002
	Q	*APETALA2 (AP2)* transcription factor	Domestication	5A	Yes	Simons et al. 2006
	Vrn-A1	MADS box transcription factor	Crop evolution	5A	No	Yan et al. 2003
	Vrn-B1	MADS box transcription factor	Crop evolution	5B	No	
	Vrn-D1	MADS box transcription factor	Crop evolution	5D	No	

[a]The genes discussed here may be viewed as either true domestication genes or as crop evolution under domestication genes. In this manuscript, we discuss these genes together. Some definitions such as the one put forward by Abbo et al. (2014) stress the importance of distinguishing between the two categories. Therefore, we make the distinctions here.

In a Tibetan weedrace (*T. aestivum* var. *tibetanum*), a brittle rachis gene Br_1 (*Br-D1*) was mapped to the short arm of chromosome 3D, suggesting that it originated from *Ae. tauschii* (Chen et al. 1998). Two other brittle rachis genes, Br_2 (*Br-A1*) and Br_3 (*Br-B1*) were mapped to the short arms of chromosomes 3A and 3B, respectively (Watanabe et al. 2002). In barley, there are two closely linked *non-brittle rachis* genes, *Btr1* and *Btr2*, which have been cloned in the homoeologous region on chromosome 3H, although they only appear to be related to each other functionally and not structurally (Pourkheirandish et al. 2015). None of the *Br* genes have been cloned in wheat, although Avni et al. (2017) have provided evidence, at the DNA sequence level, that the *Br* genes are responsible for the non-shattering phenotype in wheat through loss-of-function variants in the *Btr* homologs.

Free-threshing grain is another important domestication trait and is controlled by at least two groups of genes in wheat, the *Tenacious glumes* (*Tg*) genes and the *Q* locus on chromosome 5A. There are at least two *Tg* genes (*Tg-B1* and *Tg-D1*) in hexaploid wheat, in homoeologous positions, and a third (*Tg-A1*) is suspected on the basis of homology and some molecular evidence; however, further work is necessary to understand the role of *Tg-A1* in domestication (Faris et al. 2014). In contrast, much less is known about the homoeologous *Q* loci on chromosomes 5B and 5D. The *q* alleles at the homoeologous positions on 5B and 5D appear to have undergone pseudogenization and subfunctionalization, respectively (Zhang et al. 2011).

One of the early wheat domesticates, einkorn, was not free-threshing (Heun et al. 1997; Salamini et al. 2002); however, some einkorn accessions with soft glumes (*sog*) exist, the gene for which has been mapped to the short arm of chromosome 2A in a similar position as *Tg* in other wheats, suggesting that it is homologous to *Tg* (Taenzler et al. 2002), but this study could not localize the *sog* gene to a specific region of chromosome 2A. Comparative mapping later demonstrated that *sog* and *Tg* are not orthologs, since they occupy distinct positions on a syntenic map (Sood et al. 2009). It has been suspected by some authors that the reason for the lack of a true free-threshing character in einkorn is the ploidy level. Their hypothesis proposes that the negative pleiotropic effect of *sog* on ear length prohibited the large-scale cultivation of carriers of the mutation; however, tetraploid and hexaploid wheat do not suffer from this yield penalty, due to buffering effects from the added genomes (Salamini et al. 2002; Dubcovsky and Dvorak 2007).

The *Q* gene situated on the long arm of chromosome 5A is responsible for multiple domestication/crop evolution traits including free-threshing habit and the square spike phenotype (conferred by the *Q* allele). The wild-type (*q*) allele confers the elongated or speltoid spike phenotype. In addition, *Q* affects glume keeledness, rachis toughness, spike length and culm height (Faris et al. 2003; Simons et al. 2006). This gene is interesting because it represents a gain of function mutation. Previous work demonstrated that the *q* allele is still functional, albeit less efficient than the *Q* allele.

The *Q* allele encodes a protein that differs from the *q*-derived protein by a single amino acid, which improved homodimer formation in yeast cells. In addition, *Q* transcripts are more abundant than *q* transcripts (Simons et al. 2006). However, dimerization has not been demonstrated in wheat plants. More recently, Debernardi et al. (2017) showed that the causal polymorphism underlying the altered phenotype changed the binding site of the microRNA miR172. The alteration of miR172 is sufficient to explain the phenotypic difference between *Q* and *q* without invoking the amino acid change described by Simons et al. (2006), but also does not eliminate it entirely (Debernardi et al. 2017). Early work using cytogenetic stocks supports these more recent conclusions, demonstrating that the *Q* phenotype could be mimicked if enough copies of *q* are present (Muramatsu 1963). The *Q* gene likely originated only once, although whether *Q* arose first in tetraploid or hexaploid wheat is unknown (Simons et al. 2006).

In contrast to wheat, most barley accessions are not free threshing (covered). In covered barleys, the hull strongly adheres to the caryopsis, whereas in naked barleys the hull is dehiscent. The hulless or naked character in barley is controlled by a single gene, *naked caryopsis* (*nud*), encoding an ethylene response factor on the long arm of chromosome 7H (Taketa et al. 2008). In addition to *nud*, a gene for ease of threshability (*thresh-1*) was identified on the long arm of chromosome 1H by means of introgression mapping (Schmalenbach et al. 2011), although it has not yet been cloned. In contrast to *nud*, *thresh-1* controls the ease of separation of awns and rachis remnants from the spikelet (Schmalenbach et al. 2011). This is different

from threshability in wheat, where threshability refers to glume tenacity. Based on the non-syntenic position of both *thresh-1* and *nud* in barley with the positions of *sog, Tg* and Q in wheat, these genes have independent origins and are an example of convergent evolution (Paterson et al. 1995).

RANGE EXPANSION GENES

In contrast to their progenitors, wheat and barley are both cultivated over a wide range of latitudes. For example, the wild progenitors of wheat and barley exist in a narrow range, extending from approximately 30° N to 40°N. Modern wheat is grown as far north as the Arctic Circle and as far south as 41°S in Chile (fao.org). Barley has a similar range (croptrust.org). This range expansion may be attributed to another set of genes that altered the photoperiod response and vernalization requirements in domesticated varieties.

In barley, sequence variation in a gene involved with the photoperiod response, *Ppd-H1*, a *PSEUDO-RESPONSE REGULATOR 7* (*PRR7*), has particularly large effects on photoperiod sensitivity (Turner et al. 2005). In hexaploid wheat, the primary determinant of photoperiod response is *Ppd-D1*, an ortholog to *Ppd-H1* and confers photoperiod insensitivity, due to a deletion in a regulatory region (Beales et al. 2007). While photoperiod sensitivity genes reside in homologous regions of all three genomes of hexaploid wheat (Law et al. 1978), *Ppd-D1* is most intensively studied, followed by *Ppd-B1* (Mohler et al. 2004). Part of the reason that *Ppd-A1* is less well-studied compared to its orthologs is the lack of genetic resources needed to study it.

Evidence from chromosomal substitution lines suggest that chromosome 2A is important for photoperiod sensitivity (Law et al. 1978); however, for a long time there was no evidence of a mutant *Ppd-A1* allele affecting the photoperiod response which meant it was not possible to map the gene genetically (Beales et al. 2007). More recently, a quantitative trait locus (QTL) that could be *Ppd-A1* was identified in tetraploid (durum) wheat (Maccaferri et al. 2008). The presence of *Ppd-A1* was confirmed soon after through the identification of a mutation in the same regulatory region as that which rendered *Ppd-D1* non-functional (Wilhelm et al. 2009).

In addition to these genes, the barley homolog of *Antirrhinum CENTRORADIALIS* (*HvCEN*) was important for expansion of barley cultivation after the initial barley domestication event(s). Enrichment of pre-existing genetic variants in domesticated barley from wild barley demonstrates that the mutations underlying *HvCEN* originated before, not after, domestication (Comadran et al. 2012). The *EARLY FLOWERING 3* (*ELF3*) gene is also important to consider when discussing barley domestication. The barley gene *early maturity 8* (*EAM8*) is an ortholog of *ELF3* and is important for the transition to reproductive growth. In the context of photoperiod insensitive (*ppd-H1*) barley, the *eam8* mutation allowed for the expansion of barley cultivation into the regions of northern Europe with short growing seasons. In this sense, *eam8* should then be considered as a crop evolution under domestication gene (Faure et al. 2012; Zakhrabekova et al. 2012).

Another important trait that was altered under domestication is the modification of the vernalization requirement in domesticated genotypes of wheat and barley, both of which may be classified based on their vernalization requirement. The majority of wild barleys have a vernalization requirement. Very few wild barleys have a low vernalization requirement (Saisho et al. 2011). Those with a vernalization requirement have a winter growth habit, whereas those lacking a vernalization requirement have a spring growth habit.

The wild relatives of wheat and barley are adapted to prevent flowering from occurring when conditions are unsuitable for floral development. In wild relatives of wheat and barley, as well as in unvernalized winter varieties, *vrn1* genes are expressed at low levels, whereas in spring varieties *Vrn1* is constitutively expressed. A prolonged period of cold increases expression of *vrn1*, eventually leading to promotion of the development of reproductive tissue (Trevaskis et al. 2003; Yan et al. 2003).

Two other genes (*Vrn2* and *Vrn3*) impacting vernalization in wheat and barley also exist. *Vrn2* is on the long arm of the group 5 chromosomes and is a dominant repressor of flowering under long days though repression of *Vrn3*. Its expression is down-regulated by vernalization and short days (Dubcovsky et al. 1998; Yan et al. 2004). In contrast, *Vrn3* is an ortholog of the *Arabidopsis FLOWERING TIME* (*FT*) gene and is located on the short arm of the group 7

chromosomes (Yan et al. 2006). Repression of *Vrn2* by *Vrn1* leads to the upregulation of *Vrn3*. The interaction of the vernalization genes in domesticated wheat and barley result in two broad classes of the cereals: winter types, requiring a vernalization period and spring types, which do not require a vernalization period. The interplay of these genes with the photoperiod genes determine when an individual will flower.

In addition to the vernalization requirement, wild barley seeds have stronger dormancy than domesticated barley. This is an adaptive trait in nature, although it is detrimental in a domesticated setting since growers' demand uniform germination after planting and, in the case of malting cultivars, rapid germination is an important aspect of the malting process (Nakamura et al. 2017). In domesticated barley, dormancy may be considered as an adaptation to rainy summers since preharvest sprouting will reduce the value of the crop, but high levels of dormancy are undesirable for malting purposes (Groos et al. 2002; Torada and Amano 2002). So even after domestication, divergent selection pressures may have persisted for dormancy in barley.

YIELD AND QUALITY GENES

Modification of yield components, such as grain size and grain number, represents another achievement under domestication of wheat and barley. Barley may be classified into two different groups, based on its inflorescence type: two- and six-rowed, depending primarily on the genotype at the *six-rowed spike 1* (*vrs1*) locus on chromosome 2H (Komatsuda et al. 2007). While not a true domestication gene, in the strict sense, because two-rowed domesticated barleys are widespread, the six-rowed phenotype is uncommon in wild barley populations. In fact, wild six-rowed barleys, such as the *agriocrithon* described by Åberg (1938), are not likely to be true wild barleys; instead, these are feral or hybridized forms of domesticated barley (Zohary 1959).

The selection of six-rowed varieties by early farmers represents the potential for a three-fold increase in yield (although this is not realized in practice); therefore, it is of interest for the study of barley crop evolution. In contrast to the brittle rachis genes of barley, for which there are primarily two alleles (*Btr1*/*btr2* and *btr1*/*Btr2*) of these genes, there are multiple alleles of *vrs1*. This indicates that the six-rowed phenotype arose multiple times after fixation of the brittle rachis genes through independent mutations (Komatsuda et al. 2007).

Another important gene determining row type in barley is *INTERMEDIUM-C*, an ortholog of maize *TEOSINTE BRANCHED 1* on chromosome 4H (Ramsay et al. 2011). In general, six-rowed barley has the genotype *vrs1.a*/*Int-c.a* and two-rowed barley carried *Vrs1.b*/*int-c.b* (Ramsay et al. 2011). In wheat, *TB1* (*TB-D1* in the D genome) has also been shown to affect spike architecture through interaction with *FT1*. Wheat genotypes with higher than normal levels of *TB1-D1* expression have paired spikelets at each floret rather than a single spikelet due to extra branching. The extra branching is a result of delayed development of meristem identity tissue (Dixon et al. 2018). Homoeologs of *TB1* variants affecting spike architecture also exist in the A (*TB-A1*) and B (*TB-B1*) genomes, but variants of *TB-B1* seem to have a larger impact on spike architecture than *TB-A1* (Dixon et al. 2018). The *Vrs1* gene also exists in wheat and regulates floret number (Sakuma et al. 2018). Thus, it would be a worthwhile exercise to study the effect of *Vrs1* homoeologs in wheat.

In addition to yield-related genes, crops have evolved under domestication with respect to quality genes. In this context, quality genes refer to genes that control end-use traits like milling, baking and malting quality. A major QTL located on wheat chromosome 6BS, *Gpc-B1*, controlling grain protein, iron and zinc content has been cloned (Uauy et al. 2006). An orthologous locus has also been identified in barley (Distelfeld et al. 2008). In barley, lower protein is a trait that is important for malting. For that reason, it is clearly a trait that was selected for under domestication.

Baking quality is another important trait that evolved under domestication. Baking quality in wheat is controlled by genes known as prolamins (gliadins and glutenins) (Payne 1987). A recent assembly of the bread wheat genome (Clavijo et al. 2017) identified all previously known gluten genes, corrected 21 of these genes and identified an additional 33 genes. Thus, sequencing is useful for characterizing gluten genes to improve baking quality. Knowledge of gluten gene sequences may also be helpful in efforts to make wheat that people who suffer from celiac disease can eat, through gene editing (Sánchez-León et al. 2017).

OTHER MISCELLANEOUS GENES: CONTROLLING ORGANS INCLUDING ROOTS AND AWNS

Unlike the above ground part of plants, the root system is not well studied; nevertheless, the roots are equally important to the plant for anchoring the plant and nutrient uptake (Osmont et al. 2007). One study, in particular, elegantly demonstrated that the number of seminal roots increased from three to five as a result of wheat domestication (Golan et al. 2018). These authors showed that, in wild wheat, two root primordia are suppressed at the embryonic stage as an adaptive purpose, allowing the plants to respond to drought at early growth stages.

In wild wheats and barleys, awns provide an evolutionary advantage by facilitating seed dispersal (Sorensen 1986) and provide a mechanism for driving seeds into the soil (Elbaum et al. 2007). In barley, the awns contribute to photosynthesis (Kjack and Witters 1974), perhaps explaining why the presence of awns was preserved under domestication, although awns of domesticated barley are shorter than those of wild barley. The effect of domestication on awns in wheat does not match the clear differences between wild and domestic gene pools for other traits. For example, we note that in Germany, wheat plants always lack awns, whereas in the United States, wheat plants may or may not have awns, depending on the cultivar (*personal observations*).

Using genebank material, Börner et al. (2005) showed that accessions from northern and central Europe tend to lack awns, whereas accessions from countries in the Mediterranean basin are more likely to be awned. In addition, Rebetzke et al. (2016) showed that, depending on the environment, the presence of awns reduces grain number, but also results in increased grain size. Collectively, this suggests that the presence or absence of awns, in modern cultivars, amounts to climate adaptation or industry and consumer preference, rather than a universal effect of domestication.

In wheat, three awnless genes (*Hd, B1* and *B2*) have been mapped, but not cloned (Sourdille et al. 2008; Yoshioka et al. 2017). In barley, one of the best-characterized short awn genes is *Lks2*, which encodes a transcription factor (TF) from the SHORT INTERNODE (SHI) family (Yuo et al. 2012). In addition, the *Hooded* mutant phenotype is caused by an intronic duplication in *HvKnox3*, a homeobox gene (Müller et al. 1995). Liller et al. (2017) have also detected 12 quantitative trait loci (QTL), including a major locus on chromosome 7H, for awn length in barley using a multi-parent mapping population and array-based SNP markers combined with RNA-seq.

Another awn trait that has been affected by domestication is the presence of barbs on the awns. These barbs assist in the dispersal of seeds by attaching to animals (von Bothmer et al. 1995). Although a gene (*Raw1*) for awn barbing has been detected on chromosome 5H (Choo et al. 2001), more detailed work is still lacking. The availability of modern genomic resources ought to facilitate the detection and eventual cloning of *Raw1* and other minor genes involved with awn barbing.

GEOGRAPHY OF DOMESTICATION

The Fertile Crescent is widely accepted to be the center of origin of our cereal crops (Zohary et al. 2012), but this is a wide region and the exact location(s) of domestication has been subject to intense debate. Figure 4 shows the location of key sites and will be discussed in depth in this section. Archaeobotanical evidence and AFLP data have established the Karacadag mountains of southeast Turkey as the likely site of einkorn wheat domestication (Heun et al. 1997; Heun et al. 2008). Özkan et al. (2002) also used the AFLP approach to show that domesticated tetraploid (emmer and later durum) wheat were likely domesticated in southeast Turkey. These authors note that several other crops (pea, chickpea and lentils) were domesticated in this region with barley, which was potentially domesticated once in the Jordan valley, being a major exception. The existence of two mutant alleles of the *Btr* genes supports this region, since one of them originated in the southern Levant, which encompasses the Jordan valley (Badr et al. 2000).

New evidence suggests that domesticated barley is actually descended from a number of wild barley populations, leading to a mosaic genome (Poets et al. 2015; Pankin et al. 2018). To explain the putative domestication of barley outside the core center of southeast Turkey, Özkan et al. (2002) proposed that the practice of cultivating wild plants was an idea imported to the Israel-Jordan Valley from southeast Turkey. Follow-up work to characterize microsatellite variation

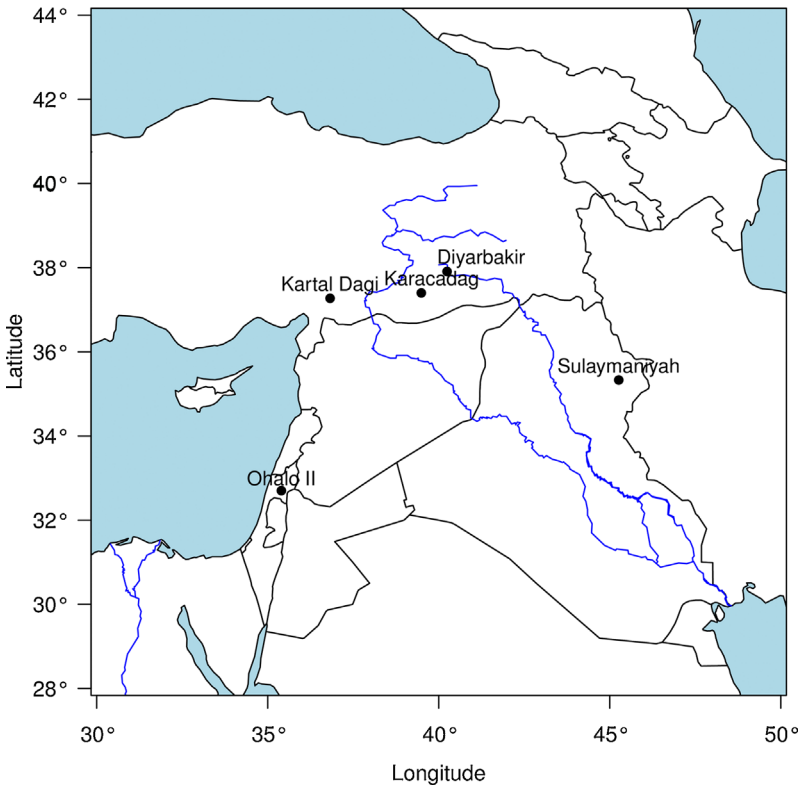

Figure 4. A map of the Fertile Crescent region featuring important sites for the domestication of wheat and barley

in the chloroplast genome by Mori et al. (2003) expanded the collection of samples to include geographic regions not included by Özkan et al. (2002). Based on the frequency of chloroplast DNA haplotypes, which were common in domesticated emmer (39.6%) and common wheat (90%) but rare (4%) in wild emmer, the Kartal Dagi region was proposed as one of two sites of emmer domestication (Mori et al. 2003).

These conclusions were called into question by Ozkan et al. (2005), who performed AFLP genotyping on a collection which included the lines previously investigated by Mori et al. (2003). To explain the rare polymorphisms in wild emmer from Kartal Dagi, Luo et al. (2007) proposed gene flow or homoplasy, although there is no conclusive evidence to know which of these, or another hypothesis, is correct. The work by Ozkan et al. (2005) and Luo et al. (2007) disagree on whether the Sulaimaniya region contributed to emmer domestication; however, both studies agree that the Dyiarbakir region contributed to emmer domestication.

Despite evidence for domestication of emmer around Karacadag, there is contradicting evidence. Notably, there has been a selective sweep in the centromeric region of chromosome 4A, which reduced genetic diversity in wild emmer populations from this region (Jorgensen et al. 2017). To explain this, Civáň et al. (2013) have suggested that wild emmer in Karacadag is feral. According to their research, wild emmer was cultivated in mixed stands prior to domestication and hybridizations arose as a result.

Others might argue against this hypothesis, because they say that this is based on the assumption that the protracted model is correct. In their view, domestication events happened at specific moments in history and are followed by crop evolution under domestication (Abbo et al. 2012). At its core, the protracted model proposes that domestication was not a rapid process, but rather involved multiple steps, over a long period, responding to changing selection pressures (Harris 1989; Fuller 2007; Brown et al. 2009; Purugganan and Fuller 2011). Archaeobotanical evidence is often in conflict with the rapid domestication scenario. For instance, artefacts from the Upper Paleolithic site of Ohalo II in Israel suggest that wild cereals were collected for baking at least 12,000 years prior to the

main agricultural revolution (Piperno et al. 2004). Other evidence demonstrates that bread was being produced 14,400 years ago, leading to the hypothesis of cultivation of cereals prior to domestication (Arranz-Otaegui et al. 2018).

There has also been considerable debate regarding the number of times and locations that barley has been domesticated. Archaeological and genetic evidence suggest that one of the origins of barley and wheat could have been the Fertile Crescent, specifically in the Israel-Jordan area in the Fertile Crescent (Badr et al. 2000). Comparative genomic analysis of ancient barley grains to modern Israeli landraces supports the Jordan valley as a center of barley domestication (Mascher et al. 2016). There are conflicting ideas over whether there has been a second domestication event in eastern Asia, specifically on the Tibetan plateau (Åberg 1938; Morrell and Clegg 2007; Dai et al. 2012). A recent archaeological study presented evidence for the presence of cultivated barley and wheat at a site in the foothills of the Zagros Mountains in Iran as early as 9,800 years ago.

One of the principal arguments in favor of a proposed second domestication center in Tibet is the existence of hulless, six-rowed barley with a brittle rachis (Dai et al. 2012), and perhaps the strongest argument for at least a diphyletic origin of barley comes from sequence divergence at the *non-brittle rachis* locus. The wild-type genotype is *Btr1*/*Btr2*, whereas the non-brittle rachis genotype is either *btr1*/*Btr2* or *Btr1*/*btr2*, with the former being more common among western accessions and the latter being more prevalent among eastern accessions. These genes are tightly linked, so the observed differences have previously been explained by two independent origins in the northern and southern Levant (Komatsuda et al. 2004; Azhaguvel and Komatsuda 2007). The *Btr1*/*btr2* genotype was later brought to East Asia by migrants (Pankin and von Korff 2017), suggesting that barley was not independently domesticated in Tibet.

The diphyletic origin of barley may also be too simplistic. Some authors have recently identified novel alleles in brittle rachis genes, supporting a more complex origin of these genes than previously understood (Civáň and Brown 2017). In the context of Tibetan six-rowed wild-growing barley, even tight linkages may be broken, given enough opportunities for recombination. Central Asia only became part of the extended range of wild barley after the last glacial maximum (Russell et al. 2014). In addition, no evidence of permanent human settlement on the Tibetan Plateau exists until 3,600 years ago (Chen et al. 2015). Without the establishment of a diverse wild barley population or a permanent human presence, a secondary domestication on the Tibetan plateau is implausible.

Recent haplotype analyses suggest that the hypothesis of the Tibetan plateau as a domestication center of barley is false (Kilian et al. 2006; Pourkheirandish et al. 2018). Further, many of the papers published in support of a second domestication center in Tibet overstate their claims, so the evidence in favor of a center of domestication in Tibet are weaker than presented. For example, Ren et al. (2013) base their claims on only two genes (a NAC transcription factor, *Nam-1* and a *Hordeum* thioredoxin-like, *HTL*); however, this is acknowledged by these authors. Alternative hypotheses are not discussed by their work. For example, nucleotide diversity (π) is lower in Tibetan wild barley than in Chinese domesticated barley (Ren et al. 2013). This matches the expectations of a genetic bottleneck resulting from a subset of domesticated barley becoming feral, yet this possibility is ignored.

The similarity of Chinese domesticated barley to Tibetan wild barley is perhaps better explained by domesticated barley becoming feral, or by introgressions of domesticated alleles into wild populations as pointed out by several authors (Badr et al. 2000; Kanazin et al. 2002). Other studies, such as Jakob et al. (2014), have shown that accessions maintained in *ex situ* Genebanks have higher rates of introgressions from domesticated varieties than in freshly collected samples, due to the use of handling protocols for inbreeding species. Although barley is an inbreeding species, outcrossing does occur, so Jakob et al. (2014) proposed that domestication studies should use freshly collected samples to make their results more reliable. The problem of domesticated introgressions into wild populations can be controlled for by excluding wild accessions with domesticated characteristics, which would indicate obvious introgressions (Badr et al. 2000); however, this does not allow for detection of cryptic introgressions which may not have visible phenotypic effects.

Morocco has also been proposed as a center of barley domestication (Molina-Cano and Conde 1980), but further evidence does not support this claim

(Blattner and Badani Méndez 2001). Finally, the Horn of Africa has been suggested to at least be a center of diversification, if not domestication (Orabi et al. 2007), but the evidence proposed in favor of domestication in Ethiopia and Eritrea is weak. Wild barley does not exist in the Horn of Africa and the extinction of a former wild barley population, caused by the overgrazing of domesticated animals, proposed by Orabi et al. (2007), does not seem plausible. The authors seem to recognize this, moderating their claim to say that the Horn of Africa "is at least a center of diversification."

Recent work suggests that, like emmer wheat, barley possesses contributions from multiple wild populations (Poets et al. 2015; Pankin et al. 2018). In addition to the evidence suggesting multiple wild populations contributed to the genomes of modern wheat and barley, it has been proposed that domestication was not a rapid process (Allaby et al. 2008) and that the rate of domestication was likely not constant (Allaby et al. 2017). These claims are controversial and, as others have pointed out, the hypothesis of a protracted domestication is based on strong assumptions that are difficult to verify. Specifically, cereals are inbreeding plants and the models chosen assume outcrossing (Heun et al. 2012). Disagreements persist and, due to the dearth of archaeobotanical data, and it is difficult to prove or disprove the protracted model. Collectively, these data suggest a diphyletic, but admixed origin of domesticated barley inside the Fertile Crescent; however, genetically distinct barley from Tibet or other regions remain useful for future barley improvement.

GENOMIC RESOURCES AND REFERENCE SEQUENCE

The earliest genomic resources available to scientists studying wheat and barley domestication were various chromosome substitution lines and aneuploid stocks. Molecular markers, such as restriction fragment length polymorphisms (RFLPs), amplified fragment length polymorphisms (AFLPs) and microsatellites/simple sequence repeat (SSR), provided extensive resources that could be used to construct genetic maps, or calculate genetic distances, for both wheat (Chao et al. 1989; Marino et al. 1996; Röder et al. 1998) and barley (Ramsay et al. 2000; Varshney et al. 2007).

The ability to measure distance, at the DNA sequence level, was crucial to domestication studies because related individuals should be more similar. Therefore, assuming no substantial genetic changes in wild populations, it is possible to trace domesticated genotypes to a potential region of origin. Further, these markers may be used to determine diversity of populations. Centers of origin of our crops should be more diverse than habitats that were colonized later, due to the length of time needed for diversity to accumulate. Additional studies, such as that by Mascher et al. (2016), are needed to better understand the genetic composition of ancient wheat and barley populations, although these studies are necessarily limited by a fragmented archeological record.

High-throughput genomic resources greatly improved the efficiency for studying wheat and barley. Single nucleotide polymorphism (SNP) arrays for wheat (Wang et al. 2014) and barley (Close et al. 2009; Comadran et al. 2012; Bayer et al. 2017) made it possible to genotype entire populations in a matter of days. However, these assays were designed using sequences derived primarily from domesticated accessions which created ascertainment bias against detection of wild alleles (Nielsen 2000). The limitations imposed by ascertainment bias may be overcome through re-sequencing studies of both wheat and barley, especially when those studies include wild genotypes; however, re-sequencing studies, such as those by Jordan et al. (2015) or Russell et al. (2016), necessitate an initial reference sequence.

The complex large genomes presented unique challenges to the generation of reference sequences of both wheat and barley. For example, the allohexaploid wheat genome is highly repetitive and its size is approximately 17 Gbp. The barley genome is smaller (~5 Gbp) but is also complex and repetitive. Complexity reduction techniques, such as exome capture or genotyping-by-sequencing, have been used to capture variation for these two crops. Jordan et al. (2015) used exome capture and genotyping-by-sequencing to study the genetic diversity of 62 bread wheat lines. In addition to describing allele frequency and distribution of SNPs and indels, they found that advantageous mutations at a single homoeologous region was often sufficient to confer a fitness benefit. Later, Russell et al. (2016) re-sequenced 267 wild barley and landrace accessions.

Their primary conclusion was that variation is related to environmental adaptation.

For a long time, the genomes of the Triticeae were considered to not be amenable to sequence assembly because of their large genome size and highly repetitive nature. Advances in sequencing technology and assembly methods have now allowed for the sequencing of these large and complex genomes. A list of completed genomes is provided in Table 2, but these are discussed in greater detail here. The first barley genome assembly, based on whole-genome shotgun sequencing of the cultivar 'Morex' was published in 2012 (International Barley Genome Sequencing Consotrium 2012), although this version was highly fragmented with an N50 of 1.4 kb. An updated version of the barley genome, based on sequencing of bacterial artificial chromosomes (BACs), was recently released (Mascher et al. 2017) and is much less fragmented with a super-scaffold N50 value of 1.9 Mb.

Multiple different wheat and wheat relative genome sequences have been published, including the genomes of the wild progenitors of hexaploid bread wheat: *T. urartu* (Ling et al. 2013; Ling et al. 2018), *Aegilops tauschii* (Jia et al. 2013; Luo et al. 2017; Zhao et al. 2017; Zimin et al. 2017b) and *T. turgidum* ssp. *dicoccoides* (Avni et al. 2017). The release of the emmer genome assembly is of great importance because it highlights the relative ease of sequencing wild relatives in the Triticeae and, due to high collinearity, future genome assemblies will benefit from pre-existing references.

Table 2. Presently available reference genomes for barley and wheat species

Crop/species	Reference
Barley (*Hordeum vulgare*)	IBGSC 2012 Mascher et al. 2017
Triticum urartu	Ling et al. 2013 Ling et al. 2018
Wild emmer (*T. turgidum*)	Avni et al. 2017
Bread wheat (*T. aestivum*)	Winfield et al. 2012 Brenchley et al. 2012 IWGSC 2014 Clavijo et al. 2017 Zimin et al. 2017a IWGSC 2018
Aegilops tauschii	Jia et al. 2013 Zimin et al. 2017b Zhao et al. 2017

The International Wheat Genome Sequencing Consortium (IWGSC) released an initial draft of the bread wheat genome in 2014 (IWGSC 2014) and will soon release an updated version (https://wheat-urgi.versailles.inra.fr/Seq-Repository/Assemblies). Clavijo et al. (2017) published a version of the hexaploid genome and a small research team released their version prior to the upcoming IWGSC release (Zimin et al. 2017a). The fact that an individual research team has been able to take on a genome such as wheat is an indication that we have arrived at a time when the availability of reference genomes will no longer be the rate-limiting step.

In the future, groups may publish multiple genomes at once and conduct pan-genomic analyses, as was recently done for rice (Stein et al. 2018). Resequencing of 66 rice accessions has revealed more than 23 million variants (Zhao et al. 2018). This study contributed greatly to the knowledge of the rice pan-genome, since the genomes were assembled independently of cultivar Nipponbare. This approach allowed divergent reads, containing important variant information for other genomes, to be retained.

Multiple reference genomes are needed to address structural variation (inversions, translocations and presence/absence variation) between genotypes. Additional reference genomes will also be useful to precisely detect domesticated introgressions into wild populations, to measure gene flow. Advances in sequencing technologies will be crucial to generating more accurate and contiguous reference genomes. For example, long reads from companies such as PacBio or Oxford Nanopore are much longer than short reads from Illumina and can, therefore, be useful to accurately sequence repeat-rich regions. However, the longer reads come with the cost of an increased error rate (Koren et al. 2012). Therefore, the use of both short and long reads may complement each other. Indeed, this is the approach used by (Zimin et al. 2017a).

GENOMICS OF CROP WILD RELATIVES

The wild progenitors of wheat, or at least close relatives in the case of the donor of the B genome of wheat, still exist in their historical range. Therefore, knowledge of these species is important for understanding wheat domestication and for exploiting these populations for beneficial alleles to improve modern wheat varieties.

Multiple genome assemblies of *Ae. tauschii*, the progenitor of the D genome, have recently been published (Luo et al. 2017; Zhao et al. 2017; Zimin et al. 2017b). Although *Ae. tauschii* is part of the primary gene pool of wheat, a recent study shows how crop wild relatives in the secondary gene pool may be exploited to recover variation lost during domestication (Gorafi et al. 2018). In that study, synthetic hexaploid wheats were created by crossing diverse *Ae. tauschii* accessions to the durum wheat cultivar Langdon. These synthetic wheats could then be directly crossed to bread wheat and the population genotyped using DArT markers in order to introgress diversity into the D genome.

The donor of the wheat B genome is not conclusively known. One probable donor is *Ae. speltoides*, though while the exact donor is still debated, the donor is accepted to belong to the sitopsis section of *Aegilops*. As such, the *sitopsis* section is a useful source for novel genes to improve modern wheat cultivars. For example, *Ae. longissima* accessions have been shown to have a high frequency of resistance to virulent races stem rust (*Puccinia graminis* f.sp. *tritici*), such as race TTKSK (Scott et al. 2014; Huang et al. 2018. More recently, Yu et al. (2017) have identified stem rust resistance genes from another member of the *sitopsis* group, *Ae. sharonensis*, by generating the first genetic map of *Ae. sharonensis* using SNPs identified by comparison with the 2014 wheat genome assembly (IWGSC 2014) and conducting genome-wide association mapping (GWAS).

APPLICATIONS

Both wild wheat and barley accessions hold the promise of novel and diverse alleles for crop improvement, as noted by Vavilov (1926). Diversity and re-sequencing studies assessed sequence diversity in wild and domesticated wheat and barley germplasm (Morrell et al. 2014; Jordan et al. 2015; Russell et al. 2016). Studies such as these have allowed for estimations of nucleotide diversity (π) and the distribution of diversity throughout the genome. In barley, neutral loci exhibit an average of 27% reduction in diversity (Russell et al. 2016), which matches an expectation based on a genetic bottleneck due to a limited number of individuals from a founder population contributing to the domesticated gene pool (Doebley et al. 2006). The dearth of diversity is particularly evident at and around known domestication genes, especially at *Btr1*/*Btr2* on chromosome 3H, highlighting strong selection pressure at these loci (Russell et al. 2016).

Indeed, many useful alleles have been identified among wild germplasm. However, wild accessions also possess deleterious traits that disrupt gains made by plant breeders, due to linkage drag. To overcome these challenges, a type of population (advanced backcross; AB) was designed to introgress wild alleles into a cultivated background (Tanksley and Nelson 1996; Matus et al. 2003). Although this type of population allowed for simultaneous detection of QTL and introgression into elite backgrounds, there is still a greater amount of linkage disequilibrium (LD) than desired, which led to the creation of the Nested Association Mapping (NAM) population design (Yu et al. 2008). Some groups have created AB-NAM barley populations including the Halle Exotic Barley 25 (HEB-25; Maurer et al. 2015) and another created using accessions from the Wild Barley Diversity Collection (WBDC; Steffenson et al. 2007; Nice et al. 2016). Additional AB-QTL studies have also been conducted in wheat (Kunert et al. 2007; Naz et al. 2008; Naz et al. 2015).

To aid in the reduction of the size of introgressed segments, genomic resources may be used to delimit the introgressions as demonstrated for *H. bulbosum* segments into *H. vulgare* (Wendler et al. 2015), the M genome of *Ae. geniculata* into wheat (Tiwari et al. 2014) and the N genome of *Ae. ventricosa* into wheat (Gao et al. 2018). Genomic resources may also be used to study transcriptomics. For example, the IWGSC (2014) established that there is no dominance between the subgenomes of wheat at the transcriptional level and there is little regulation of genes between the three genomes. More recent work has shown coordination of homoeologs, potentially allowing for the development of new functions for homoeologs (Ramírez-González et al. 2018).

CONCLUSION

The genomes of wheat and barley had long been considered to be intractable to large-scale genome analyses; however, technological advancements have made sequencing these large and complex genomes possible. Prior to the advent of whole-genome studies, molecular markers enabled the first attempts to use

genetics to characterize major domestication genes and to establish the domestication centers of our crops, including wheat and barley. These studies, while fruitful, were inherently limited due to the limited number of available markers and the full representation of the genomes of these crops.

The availability of reference genomes for both wheat and barley facilitates the discovery and use of polymorphisms to answer open questions in domestication genomics. Re-sequencing studies employing complexity reduction techniques, such as that by Russell et al. (2016), advanced large-scale genomic studies in barley. However, the reduction in cost of whole-genome shotgun (WGS) sequencing has made this a viable option to capture the full genomic diversity in a limited number of samples, not just in coding regions. This is of critical importance for non-coding regulatory regions. In the future, it will be possible to answer presently unresolved questions due to the generation of additional reference sequences of diverse wheats and barleys. This has already been achieved for *Oryza* species, for which 13 genomes of wild and domesticated rice species have been published (Stein et al. 2018).

Among the research questions or areas that stand to benefit from additional reference sequences are: (1) if structural and gene content variation have been impacted by domestication, (2) how sequence data can improve selection scans, (3) improvement of demographic inference through improved contextualization of markers, and (4) high-resolution detection of crop-wild introgressions. Additional reference genomes will enable the study of structural variation between the wild and domestic forms of wheat and barley. For example, structural variation exists between individual maize and teosinte accessions. Although this type of variation does not seem to be particularly important for maize domestication (Swanson-Wagner et al. 2010), this should be investigated in wheat and barley.

Selection scans are useful for detecting loci that have experienced selection as well as the strength of these selections. For example, Pankin et al. (2018) have recently published such work in barley using targeted resequencing. Based on their results, they claim that additional domestication genes remain undiscovered. The number of wild (344) and domesticated (89) accessions from that work is significant and the number of loci (1,666 total) is sufficient to support their claims. However, additional references would still improve accuracy of selection estimates, especially in genomic regions not included in the enrichment-based resequencing assay, through improved estimates of nucleotide diversity and recombination rates.

The generation of additional reference genomes may also confirm and/or resolve some of the findings concerning demography. In barley, this relates to whether domesticated barley arose from multiple proto-domesticated lineages (Poets et al. 2015; Pankin et al. 2018). In wheat, there are more outstanding questions, including the precise origin(s) of spelt and emmer. Additional sequences will also enable the detection of introgressions of wild alleles into domesticated forms (and vice versa). Despite low out-crossing rates, we know that wild crop relatives have introgressions from domesticated forms, particularly during maintenance in *ex situ* genebanks (Jakob et al. 2014). These introgressions could then be filtered out of datasets so that they do not bias the results.

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REFERENCES

Abbo S, Lev-Yadun S, Gopher A (2012) Plant domestication and crop evolution in the near east: On events and processes. **Crit Rev Plant Sci** 31: 241–257

Abbo S, van-Oss RP, Gopher A, Saranga Y, Ofner I, Peleg Z (2014) Plant domestication versus crop evolution: A conceptual framework for cereals and grain legumes. **Trends Plant Sci** 19: 351–360

Åberg E (1938) *Hordeum agriocrithon* nova sp., a wild six-rowed barley. **Ann Agric Coll Sweden** 6: 159–216

Allaby RG, Fuller DQ, Brown TA (2008) The genetic expectations of a protracted model for the origins of domesticated crops. **Proc Natl Acad Sci USA** 105: 13982–13986

Allaby RG, Stevens C, Lucas L, Maeda O, Fuller DQ (2017) Geographic mosaics and changing rates of cereal domestication. **Philos Trans R Soc B Biol Sci** 372: 20160429

Arranz-Otaegui A, Carretero LG, Ramsey MN, Fuller DQ, Richter T (2018) Archaeobotanical evidence reveals the origins of bread 14,400 years ago in northeastern Jordan. **Proc Natl Acad Sci USA** 115: 7925–7930

Avni R, Nave M, Barad O, Baruch K, Twardziok SO, Gundlach H, Hale I, Mascher M, Spannagl M, Wiebe K, Jordan KW, Golan G, Deek J, Ben-Zvi B, Ben-Zvi G, Himmelbach A, MacLachlan RP, Sharpe AG, Fritz A, Ben-David R, Budak H, Fahima T, Korol A, Faris JD, Hernandez A, Mikel MA, Levy AA, Steffenson B, Maccaferri M, Tuberosa R, Cattivelli L, Faccioli P, Ceriotti A, Kashkush K, Pourkheirandish M, Komatsuda T, Eilam T, Sela H, Sharon A, Ohad N, Chamovitz DA, Mayer KFX, Stein N, Ronen G, Peleg Z, Pozniak CJ, Akhunov ED, Distelfeld A (2017) Wild emmer genome architecture and diversity elucidate wheat evolution and domestication. **Science** 357: 93–97

Azhaguvel P, Komatsuda T (2007) A phylogenetic analysis based on nucleotide sequence of a marker linked to the brittle rachis locus indicates a diphyletic origin of barley. **Ann Bot** 100: 1009–1015

Badr A, Muller K, Schafer R, El Rabey HE, Effgen S, Ibrahim HH, Pozzi C, Rohde W, Salamini F (2000) On the origin and domestication history of barley (*Hordeum vulgare*). **Mol Biol Evol** 17: 499–510

Bayer MM, Rapazote-Flores P, Ganal M, Hedley PE, Macaulay M, Plieske J, Ramsay L, Russell J, Shaw PD, Thomas W, Waugh R (2017) Development and evaluation of a barley 50k iSelect SNP array. **Front Plant Sci** 8: 1792

Beales J, Turner A, Griffiths S, Snape JW, Laurie DA (2007) A pseudo-response regulator is misexpressed in the photoperiod insensitive *Ppd-D1a* mutant of wheat (*Triticum aestivum* L.). **Theor Appl Genet** 115: 721–733

Blake NK, Lehfeldt BR, Lavin M, Talbert LE (1999) Phylogenetic reconstruction based on low copy DNA sequence data in an allopolyploid: The B genome of wheat. **Genome** 42: 351–360

Blatter RHE, Jacomet S, Schlumbaum A (2004) About the origin of European spelt (*Triticum spelta* L.): Allelic differentiation of the HMW Glutenin B1-1 and A1-2 subunit genes. **Theor Appl Genet** 108: 360–367

Blattner FR, Badani Méndez AG (2001) RAPD data do not support a second centre of barley domestication in Morocco. **Genet Resour Crop Evol** 48: 13–19

von Bothmer R, Jacobsen N, Baden C, Jorgensen R, Linde-Laursen I (1995) *An Ecogeographical Study of The Genus Hordeum*, 2nd edn. Rome: International Plant Genetic Resources Institute

Börner A, Schäfer M, Schmidt A, Grau M, Vorwald J (2005) Associations between geographical origin and morphological characters in bread wheat (*Triticum aestivum* L.). **Plant Genet Resour** 3: 360–372

Brenchley R, Spannagl M, Pfeifer M, Barker GLA, D'Amore R, Allen AM, McKenzie N, Kramer M, Kerhornou A, Bolser D, Kay S, Waite D, Trick M, Bancroft I, Gu Y, Huo N, Luo M-C, Sehgal S, Gill B, Kianian S, Anderson O, Kersey P, Dvorak J, McCombie R, Hall A, Mayer KFX, Edwards KJ, Bevan MW, Hall N (2012) Analysis of the bread wheat genome using whole-genome shotgun sequencing. **Nature** 491: 705–710

Brown TA, Jones MK, Powell W, Allaby RG (2009) The complex origins of domesticated crops in the Fertile Crescent. **Trends Ecol Evol** 24: 103–109

Chalupska D, Lee HY, Faris JD, Evrard A, Chalhoub B, Haselkorn R, Gornicki P (2008) *Acc* homoeoloci and the evolution of wheat genomes. **Proc Natl Acad Sci USA** 105: 9691–9696

Chao S, Sharp PJ, Worland AJ, Warham EJ, Koebner RMD, Gale MD (1989) RFLP-based genetic maps of wheat homoeologous group 7 chromosomes. **Theor Appl Genet** 78: 495–504

Chen FH, Dong GH, Zhang DJ, Liu XY, Jia X, An CB, Ma MM, Xie YW, Barton L, Ren XY, Zhao ZJ, Wu XH, Jones MK (2015) Agriculture facilitated permanent human occupation of the Tibetan Plateau after 3600 B.P. **Science** 347: 248–250

Chen QF, Yen C, Yang JL (1998) Chromosome location of the gene for brittle rachis in the Tibetan weedrace of common wheat. **Genet Resour Crop Evol** 45: 407–410

Choo TM, Ho KM, Martin RA (2001) Genetic analysis of a hulless×covered cross of barley using doubled-haploid lines. **Crop Sci** 41: 1021–1026

Civáň P, Brown TA (2017) A novel mutation conferring the nonbrittle phenotype of cultivated barley. **New Phytol** 214: 468–472

Civáň P, Ivaničová Z, Brown TA (2013) Reticulated origin of domesticated emmer wheat supports a dynamic model for the emergence of agriculture in the Fertile Crescent. **PLoS ONE** 8: e81955

Clavijo BJ, Venturini L, Schudoma C, Accinelli GG, Kaithakottil G, Wright J, Borrill P, Kettleborough G, Heavens D, Chapman H, Lipscombe J, Barker T, Lu F-H, McKenzie N, Raats D, Ramirez-Gonzalez RH, Coince A, Peel N, Percival-Alwyn L, Duncan O, Trösch J, Yu G, Bolser DM, Namaati G, Kerhornou A, Spannagl M, Gundlach H, Haberer G, Davey RP, Fosker C, Palma FD, Phillips AL, Millar AH, Kersey PJ, Uauy C, Krasileva KV, Swarbreck D, Bevan MW, Clark MD (2017) An improved assembly and annotation of the allohexaploid wheat genome identifies complete families of agronomic genes and provides genomic evidence for chromosomal translocations. **Genome Res** 27: 885–896

Close TJ, Bhat PR, Lonardi S, Wu Y, Rostoks N, Ramsay L, Druka A, Stein N, Svensson JT, Wanamaker S, Bozdag S, Roose ML, Moscou MJ, Chao S, Varshney RK, Szűcs P, Sato K, Hayes PM, Matthews DE, Kleinhofs A, Muehlbauer GJ, DeYoung J, Marshall DF, Madishetty K, Fenton RD, Condamine P, Graner A, Waugh R (2009) Development and implementation of high-throughput SNP genotyping in barley. **BMC Genomics** 10: 582

Comadran J, Kilian B, Russell J, Ramsay L, Stein N, Ganal M, Shaw P, Bayer M, Thomas W, Marshall D, Hedley P, Tondelli A, Pecchioni N, Francia E, Korzun V, Walther A, Waugh R (2012) Natural variation in a homolog of *Antirrhinum CENTRORADIALIS* contributed to spring growth habit and environmental adaptation in cultivated barley. **Nat Genet** 44: 1388–1393

Dai F, Nevo E, Wu D, Comadran J, Zhou M, Qiu L, Chen Z, Beiles A, Chen G, Zhang G (2012) Tibet is one of the centers of domestication of cultivated barley. **Proc Natl Acad Sci USA** 109: 16969–16973

Debernardi JM, Lin H, Chuck G, Faris JD, Dubcovsky J (2017) microRNA172 plays a crucial role in wheat spike

morphogenesis and grain threshability. **Development** 144: 1966–1975

Distelfeld A, Korol A, Dubcovsky J, Uauy C, Blake T, Fahima T (2008) Colinearity between the barley grain protein content (GPC) QTL on chromosome arm 6HS and the wheat *Gpc-B1* region. **Mol Breed** 22: 25–38

Dixon LE, Greenwood JR, Bencivenga S, Zhang P, Cockram J, Mellers G, Ramm K, Cavanagh C, Swain SM, Boden SA (2018) TEOSINTE BRANCHED1 regulates inflorescence architecture and development in bread wheat (*Triticum aestivum* L.). **Plant Cell** 30: 563–581

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

Dubcovsky J, Lijavetzky D, Appendino L, Tranquilli G (1998) Comparative RFLP mapping of *Triticum monococcum* genes controlling vernalization requirement. **Theor Appl Genet** 97: 968–975

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

Dvorak J, Deal KR, Luo MC, You FM, von Borstel K, Dehghani H (2012) The origin of spelt and free-threshing hexaploid wheat. **J Hered** 103: 426–441

Dvořák J, Terlizzi P, Zhang HB, Resta P (1993) The evolution of polyploid wheats: Identification of the A genome donor species. **Genome** 36: 21–31

Elbaum R, Zaltzman L, Burgert I, Fratzl P (2007) The role of wheat awns in the seed dispersal unit. **Science** 316: 884–886

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

Faris JD, Zhang Z, Chao S (2014) Map-based analysis of the tenacious glume gene *Tg-B1* of wild emmer and its role in wheat domestication. **Gene** 542: 198–208

Faure S, Turner AS, Gruszka D, Christodoulou V, Davis SJ, von Korff M, Laurie DA (2012) Mutation at the circadian clock gene *EARLY MATURITY* 8 adapts domesticated barley (*Hordeum vulgare*) to short growing seasons. **Proc Natl Acad Sci USA** 109: 8328–8333

Fuller DQ (2007) Contrasting patterns in crop domestication and domestication rates: Recent achaeobotanical insights from the old world. **Ann Bot** 100: 903–924

Gao L, Dorn K, Rife TW, Wang X, Lemes C, Clinesmith M, Silva P, Fritz A, Stein N, Mascher M, Poland J (2018) Completion of the 'Jagger' wheat genome leads to identification of *Aegilops ventricosa* 2NS translocation and its impact in wheat breeding. (https://pag.confex.com/pag/xxvi/meetingapp.cgi/Paper/30261)

Glemin S, Scornavacca C, Dainat J, Burgarella C, Viader V, Ardisson M, Sarah G, Santoni S, David J, Ranwez V (2018) Pervasive hybridizations in the history of wheat relatives. **bioRxiv** 300848 doi: 10.1101/300848

Golan G, Hendel E, Méndez Espitia GE, Schwartz N, Peleg Z (2018) Activation of seminal root primordia during wheat domestication reveals underlying mechanisms of plant resilience. **Plant Cell Environ** 41: 755–766

Gorafi YSA, Kim JS, Elbashir AAE, Tsujimoto H (2018) A population of wheat multiple synthetic derivatives: An effective platform to explore, harness and utilize genetic diversity of *Aegilops tauschii* for wheat improvement. **Theor Appl Genet** 131: 1615–1626

Groos C, Gay G, Perretant MR, Gervais L, Bernard M, Dedryver F, Charmet G (2002) Study of the relationship between pre-harvest sprouting and grain color by quantitative trait loci analysis in a white × red grain bread-wheat cross. **Theor Appl Genet** 104: 39–47

Harlan JR, Zohary D (1966) Distribution of wild wheats and barley. **Science** 153: 1074–1080

Harris DR (1989) An evolutionary continuum of people-plant interaction. In: Harris DR, Hillman GC, eds. *Foraging and Farming: The Evolution of Plant Exploitation*. Routledge, London. pp. 11–26

Heun M, Abbo S, Lev-Yadun S, Gopher A (2012) A critical review of the protracted domestication model for Near-Eastern founder crops: Linear regression, long-distance gene flow, archaeological, and archaeobotanical evidence. **J Exp Bot** 63: 4333–4341

Heun M, Haldorsen S, Vollan K (2008) Reassessing domestication events in the Near East: Einkorn and *Triticum urartu*. **Genome** 51: 444–451

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

Huang S, Steffenson B, Sela H, Stinebaugh K (2018) Resistance of *Aegilops longissima* to the rusts of wheat. **Plant Dis** 102: 1124–1135

International Barley Genome Sequencing C (2012) A physical, genetic and functional sequence assembly of the barley genome. **Nature** 491: 711–716

International Wheat Genome Sequencing Consortium (2014) A chromosome-based draft sequence of the hexaploid bread wheat *Triticum aestivum* genome. **Science** 345: 1251788

International Wheat Genome Sequencing Consortium (2018) Shifting the limits in wheat research and breeding using a fully annotated reference genome. **Science** 361: eaar7191

Jakob SS, Rödder D, Engler JO, Shaaf S, Özkan H, Blattner FR, Kilian B (2014) Evolutionary history of wild barley (*Hordeum vulgare* subsp. *spontaneum*) analyzed using multilocus sequence data and paleodistribution modeling. **Genome Biol Evol** 6: 685–702

Jia J, Zhao S, Kong X, Li Y, Zhao G, He W, Appels R, Pfeifer M, Tao Y, Zhang X, Jing R, Zhang C, Ma Y, Gao L, Gao C, Spannagl M, Mayer KFX, Li D, Pan S, Zheng F, Hu Q, Xia X, Li J, Liang Q, Chen J, Wicker T, Gou C, Kuang H, He G, Luo Y, Keller B, Xia Q, Lu P, Wang J, Zou H, Zhang R, Xu J, Gao J, Middleton C, Quan Z, Liu G, Wang J, International Wheat Genome Sequencing C, Yang H, Liu X, He Z, Mao L, Wang J (2013) *Aegilops tauschii* draft genome sequence reveals a gene repertoire for wheat adaptation. **Nature** 496: 91–95

Jordan KW, Wang S, Lun Y, Gardiner LJ, MacLachlan R, Hucl P, Wiebe K, Wong D, Forrest KL, Sharpe AG, Sidebottom CH, Hall N, Toomajian C, Close T, Dubcovsky J, Akhunova A, Talbert L, Bansal UK, Bariana HS, Hayden MJ, Pozniak C, Jeddeloh JA, Hall A, Akhunov E (2015) A haplotype map of allohexaploid wheat reveals distinct patterns of selection on homoeologous genomes. **Genome Biol** 16: 48

Jorgensen C, Luo MC, Ramasamy R, Dawson M, Gill BS, Korol AB, Distelfeld A, Dvorak J (2017) A high-density genetic map of wild emmer wheat from the Karaca Dağ region provides new evidence on the structure and evolution of wheat chromosomes. **Front Plant Sci** 8: 1798

Kanazin V, Talbert H, See D, DeCamp P, Nevo E, Blake T (2002) Discovery and assay of single-nucleotide polymorphisms in barley (*Hordeum vulgare*). **Plant Mol Biol** 48: 529–537

Kilian B, Özkan H, Kohl J, von Haeseler A, Barale F, Deusch O, Brandolini A, Yucel C, Martin W, Salamini F (2006) Haplotype structure at seven barley genes: Relevance to gene pool bottlenecks, phylogeny of ear type and site of barley domestication. **Mol Genet Genomics** 276: 230–241

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

Kjack JL, Witters RE (1974) Physiological activity of awns in isolines of Atlas Barley1. **Crop Sci** 14: 243–248

Komatsuda T, Maxim P, Senthil N, Mano Y (2004) High-density AFLP map of nonbrittle rachis 1 (*btr1*) and 2 (*btr2*) genes in barley (*Hordeum vulgare* L.). **Theor Appl Genet** 109: 986–995

Komatsuda T, Pourkheirandish M, He C, Azhaguvel P, Kanamori H, Perovic D, Stein N, Graner A, Wicker T, Tagiri A, Lundqvist U, Fujimura T, Matsuoka M, Matsumoto T, Yano M (2007) Six-rowed barley originated from a mutation in a homeodomain-leucine zipper I-class homeobox gene. **Proc Natl Acad Sci USA** 104: 1424–1429

Koren S, Schatz MC, Walenz BP, Martin J, Howard JT, Ganapathy G, Wang Z, Rasko DA, McCombie WR, Jarvis ED, Phillippy AM (2012) Hybrid error correction and *de novo* assembly of single-molecule sequencing reads. **Nat Biotechnol** 30: 693–700

Kunert A, Naz AA, Dedeck O, Pillen K, Léon J (2007) AB-QTL analysis in winter wheat: I. Synthetic hexaploid wheat (*T. turgidum* ssp. *dicoccoides* × *T. tauschii*) as a source of favourable alleles for milling and baking quality traits. **Theor Appl Genet** 115: 683–695

Law CN, Sutka J, Worland AJ (1978) A Genetic study of day-length response in wheat. **Heredity** 41: 185–191

Liller CB, Walla A, Boer MP, Hedley P, Macaulay M, Effgen S, von Korff M, van Esse GW, Koornneef M (2017) Fine mapping of a major QTL for awn length in barley using a multiparent mapping population. **Theor Appl Genet** 130: 269–281

Ling H-Q, Zhao S, Liu D, Wang J, Sun H, Zhang C, Fan H, Li D, Dong L, Tao Y, Gao C, Wu H, Li Y, Cui Y, Guo X, Zheng S, Wang B, Yu K, Liang Q, Yang W, Lou X, Chen J, Feng M, Jian J, Zhang X, Luo G, Jiang Y, Liu J, Wang Z, Sha Y, Zhang B, Wu H, Tang D, Shen Q, Xue P, Zou S, Wang X, Liu X, Wang F, Yang Y, An X, Dong Z, Zhang K, Zhang X, Luo M-C, Dvorak J, Tong Y, Wang J, Yang H, Li Z, Wang D, Zhang A, Wang J (2013) Draft genome of the wheat A-genome progenitor *Triticum urartu*. **Nature** 496: 87–90

Ling HQ, Ma B, Shi X, Liu H, Dong L, Sun H, Cao Y, Gao Q, Zheng S, Li Y, Yu Y, Du H, Qi M, Li Y, Lu H, Yu H, Cui Y, Wang N, Chen C, Wu H, Zhao Y, Zhang J, Li Y, Zhou W, Zhang B, Hu W, van Eijk MJT, Tang J, Witsenboer HMA, Zhao S, Li Z, Zhang A, Wang D, Liang C (2018) Genome sequence of the progenitor of wheat A subgenome *Triticum urartu*. **Nature** 557: 424–428

Longin CFH, Würschum T (2016) Back to the Future–Tapping into ancient grains for food diversity. **Trends Plant Sci** 21: 731–737

Luo MC, Gu YQ, Puiu D, Wang H, Twardziok SO, Deal KR, Huo N, Zhu T, Wang L, Wang Y, McGuire PE, Liu S, Long H, Ramasamy RK, Rodriguez JC, Van SL, Yuan L, Wang Z, Xia Z, Xiao L, Anderson OD, Ouyang S, Liang Y, Zimin AV, Pertea G, Qi P, Bennetzen JL, Dai X, Dawson MW, Müller H-G, Kugler K, Rivarola-Duarte L, Spannagl M, Mayer KFX, Lu F-H, Bevan MW, Leroy P, Li P, You FM, Sun Q, Liu Z, Lyons E, Wicker T, Salzberg SL, Devos KM, Dvořák J (2017) Genome sequence of the progenitor of the wheat D genome *Aegilops tauschii*. **Nature** 551: 498–502

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

Maccaferri M, Sanguineti MC, Corneti S, Ortega JLA, Salem MB, Bort J, DeAmbrogio E, del Moral LFG, Demontis A, El-Ahmed A, Maalouf F, Machlab H, Martos V, Moragues M, Motawaj J, Nachit M, Nserallah N, Ouabbou H, Royo C, Slama A, Tuberosa R (2008) Quantitative trait loci for grain yield and adaptation of durum wheat (*Triticum durum* Desf.) across a wide range of water availability. **Genetics** 178: 489–511

Marcussen T, Sandve SR, Heier L, Spannagl M, Pfeifer M, Jakobsen KS, Wulff BBH, Steuernagel B, Mayer KFX, Olsen OA (2014) Ancient hybridizations among the ancestral genomes of bread wheat. **Science** 345: 1250092

Marino CL, Tuleen NA, Hart GE, Nelson JC, Sorrells ME, Lu YH, Leroy P, Lopes CR (1996) Molecular genetic maps of the group 6 chromosomes of hexaploid wheat (*Triticum aestivum* L. em. Thell.). **Genome** 39: 359–366

Mascher M, Gundlach H, Himmelbach A, Beier S, Twardziok SO, Wicker T, Radchuk V, Dockter C, Hedley PE, Russell J, Bayer M, Ramsay L, Liu H, Haberer G, Zhang XQ, Zhang Q, Barrero RA, Li L, Taudien S, Groth M, Felder M, Hastie A, Šimková H, Staňková H, Vrána J, Chan S, Muñoz-Amatriaín M, Ounit R, Wanamaker S, Bolser D, Colmsee C, Schmutzer T, Aliyeva-Schnorr L, Grasso S, Tanskanen J, Chailyan A, Sampath D, Heavens D, Clissold L, Cao S, Chapman B, Dai F, Han Y, Li H, Li X, Lin C, McCooke JK, Tan C, Wang P, Wang S, Yin S, Zhou G, Poland JA, Bellgard MI, Borisjuk L, Houben A, Doležel J, Ayling S, Lonardi S, Kersey P, Langridge P,

Muehlbauer GJ, Clark MD, Caccamo M, Schulman AH, Mayer KFX, Platzer M, Close TJ, Scholz U, Hansson M, Zhang G, Braumann I, Spannagl M, Li C, Waugh R, Stein N (2017) A chromosome conformation capture ordered sequence of the barley genome. **Nature** 544: 427–433

Mascher M, Schuenemann VJ, Davidovich U, Marom N, Himmelbach A, Hübner S, Korol A, David M, Reiter E, Riehl S, Schreiber M, Vohr SH, Green RE, Dawson IK, Russell J, Kilian B, Muehlbauer GJ, Waugh R, Fahima T, Krause J, Weiss E, Stein N (2016) Genomic analysis of 6,000-year-old cultivated grain illuminates the domestication history of barley. **Nat Genet** 48: 1089–1093

Matus I, Corey A, Filichkin T, Hayes PM, Vales MI, Kling J, Riera-Lizarazu O, Sato K, Powell W, Waugh R (2003) Development and characterization of recombinant chromosome substitution lines (RCSLs) using *Hordeum vulgare* subsp. *spontaneum* as a source of donor alleles in a *Hordeum vulgare* subsp. vulgare background. **Genome** 46: 1010–1023

Maurer A, Draba V, Jiang Y, Schnaithmann F, Sharma R, Schumann E, Kilian B, Reif JC, Pillen K (2015) Modelling the genetic architecture of flowering time control in barley through nested association mapping. **BMC Genomics** 16: 290

Mohler V, Lukman R, Ortiz-Islas S, William M, Worland AJ, van Beem J, Wenzel G (2004) Genetic and physical mapping of photoperiod insensitive gene *Ppd-B1* in common wheat. **Euphytica** 138: 33–40

Molina-Cano JL, Conde J (1980) *Hordeum spontaneum* C. Koch em. Bacht, collected in southern Morocco. **Barley Genet Newsl** 10: 44–47

Mori N, Ishi T, Ishido T, Hirosawa S, Watatani H, Kawahara T, Nesbitt M, Belay G, Takumi S, Ogihara Y, Nakamura C (2003) Origins of domesticated emmer and common wheat inferred from chloroplast DNA fingerprinting. **Tenth Int Wheat Genet Symp** 2003: 25–28

Morrell PL, Clegg MT (2007) Genetic evidence for a second domestication of barley *Hordeum vulgare* east of the Fertile Crescent. **Proc Natl Acad Sci USA** 104: 3289–3294

Morrell PL, Gonzales AM, Meyer KKT, Clegg MT (2014) Resequencing data indicate a modest effect of domestication on diversity in barley: A cultigen with multiple origins. **J Hered** 105: 253–264

Müller KJ, Romano N, Gerstner O, Garcia-Marotot F, Pozzi C, Salamini F, Rohde W (1995) The barley Hooded mutation caused by a duplication in a homeobox gene intron. **Nature** 374: 727–730

Müller T, Schierscher-Viret B, Fossati D, Brabant C, Schori A, Keller B, Krattinger SG (2018) Unlocking the diversity of genebanks: Whole-genome marker analysis of Swiss bread wheat and spelt. **Theor Appl Genet** 131: 407–416

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

Nakamura S, Pourkheirandish M, Morishige H, Sameri M, Sato K, Komatsuda T (2017) Quantitative trait loci and maternal effects affecting the strong grain dormancy of wild barley (*Hordeum vulgare* ssp. *spontaneum*). **Front Plant Sci** 8: 1840

Naz AA, Kunert A, Lind V, Pillen K, Léon J (2008) AB-QTL analysis in winter wheat: II. Genetic analysis of seedling and field resistance against leaf rust in a wheat advanced backcross population. **Theor Appl Genet** 116: 1095–1104

Naz AA, Klaus M, Pillen K, Léon J (2015) Genetic analysis and detection of new QTL alleles for *Septoria tritici* blotch resistance using two advanced backcross wheat populations. **Plant Breed** 134: 514–519

Nice LM, Steffenson BJ, Brown-Guedira GL, Akhunov ED, Liu C, Kono TJY, Morrell PL, Blake TK, Horsley RD, Smith KP, Muehlbauer GJ (2016) Development and genetic characterization of an advanced backcross-nested association mapping (AB-NAM) population of wild × cultivated barley. **Genetics** 203: 1453–1467

Nielsen R (2000) Estimation of population parameters and recombination rates from single nucleotide polymorphisms. **Genetics** 154: 931–942

Orabi J, Backes G, Wolday A, Yahyaoui A, Jahoor A (2007) The Horn of Africa as a centre of barley diversification and a potential domestication site. **Theor Appl Genet** 114: 1117–1127

Osmont KS, Sibout R, Hardtke CS (2007) Hidden branches: Developments in root system architecture. **Annu Rev Plant Biol** 58: 93–113

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

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

Özkan H, Willcox G, Graner A, Salamini F, Kilian B (2011) Geographic distribution and domestication of wild emmer wheat (*Triticum dicoccoides*). **Genet Resour Crop Evol** 58: 11–53

Pankin A, Altmüller J, Becker C, Korff M (2018) Targeted resequencing reveals genomic signatures of barley domestication. **New Phytol** 218: 1247–1259

Pankin A, von Korff M (2017) Co-evolution of methods and thoughts in cereal domestication studies: A tale of barley (*Hordeum vulgare*). **Curr Opin Plant Biol** 36: 15–21

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

Payne PI (1987) Genetics of wheat storage proteins and the effect of allelic variation on bread-making quality. **Annu Rev Plant Physiol** 38: 141–153

Peng J, Sun D, Nevo E (2011) Wild emmer wheat, *Triticum dicoccoides*, occupies a pivotal position in wheat domestication process. **Aust J Crop Sci** 5: 1127–1143

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

Poets AM, Fang Z, Clegg MT, Morrell PL (2015) Barley landraces are characterized by geographically heterogeneous genomic origins. **Genome Biol** 16: 173

Pont C, Salse J (2017) Wheat paleohistory created asymmetrical genomic evolution. **Curr Opin Plant Biol** 36: 29–37

Pourkheirandish M, Hensel G, Kilian B, Senthil N, Chen G, Sameri M, Azhaguvel P, Sakuma S, Dhanagond S, Sharma R, Mascher M, Himmelbach A, Gottwald S, Nair Sudha K, Tagiri A, Yukuhiro F, Nagamura Y, Kanamori H, Matsumoto T, Willcox G, Middleton Christopher P, Wicker T, Walther A, Waugh R, Fincher Geoffrey B, Stein N, Kumlehn J, Sato K, Komatsuda T (2015) Evolution of the grain dispersal system in barley. **Cell** 162: 527–539

Pourkheirandish M, Kanamori H, Wu J, Sakuma S, Blattner FR, Komatsuda T (2018) Elucidation of the origin of "*agriocrithon*" based on domestication genes questions the hypothesis that Tibet is one of the centers of barley domestication. **Plant J** 94: 525–534

Purugganan MD, Fuller DF (2011) Archeaological data reveal slow rates of evolution during plant domestication. **Evolution** 65: 171–183

Ramírez-González RH, Borrill P, Lang D, Harrington SA, Brinton J, Venturini L, Davey M, Jacobs J, van Ex F, Pasha A, Khedikar Y, Robinson SJ, Cory AT, Florio T, Concia L, Juery C, Shoonbeek H, Steuernagel B, Xiang D, Ridout CJ, Chalhoub B, Mayer KFX, Benhamed M, Latrasse D, Bendahmane A, IWGSC, Wulff BBH, Appels R, Tiwari V, Dalta R, Choulet F, Pozniak CJ, Provart NJ, Sharpe AG, Paux E, Spannagl M, Bräutigam A, Uauy C (2018) The transcriptional landscape of polyploid wheat. **Science** 361: 6089

Ramsay L, Comadran J, Druka A, Marshall DF, Thomas WTB, Macaulay M, MacKenzie K, Simpson C, Fuller J, Bonar N, Hayes PM, Lundqvist U, Franckowiak JD, Close TJ, Muehlbauer GJ, Waugh R (2011) *INTERMEDIUM-C*, a modifier of lateral spikelet fertility in barley, is an ortholog of the maize domestication gene *TEOSINTE BRANCHED 1*. **Nat Genet** 43: 169–172

Ramsay L, Macaulay M, Ivanissevich S, MacLean K, Cardle L, Fuller J, Edwards KJ, Tuvesson S, Morgante M, Massari A, Maestri E, Marmiroli N, Sjakste T, Ganal M, Powell W, Waugh R (2000) A simple sequence repeat-based linkage map of barley. **Genetics** 156: 1997–2005

Rebetzke GJ, Bonnett DG, Reynolds MP, Awns reduce grain number to increase grain size and harvestable yield in irrigated and rainfed spring wheat, **J Exp Bot** 67: 2573–2586

Ren X, Nevo E, Sun D, Sun G (2013) Tibet as a potential domestication center of cultivated barley of China. **PLoS ONE** 8: e62700

Röder MS, Korzun V, Wendehake K, Plaschke J, Tixier MH, Leroy P, Ganal MW (1998) A microsatellite map of wheat. **Genetics** 149: 2007–2023

Russell J, Zonneveld van M, Dawson IK, Booth A, Waugh R, Steffenson B (2014) Genetid diversity and ecological niche modelling of wild barley: Refugia, large-scale post-LGM range expansion and limited mid-future climate threats. **PLoS ONE** 9: e86021

Russell J, Mascher M, Dawson IK, Kyriakidis S, Calixto C, Freund F, Bayer M, Milne I, Marshall-Griffiths T, Heinen S, Hofstad A, Sharma R, Himmelbach A, Knauft M, van Zonneveld M, Brown JWS, Schmid K, Kilian B, Muehlbauer GJ, Stein N, Waugh R (2016) Exome sequencing of geographically diverse barley landraces and wild relatives gives insights into environmental adaptation. **Nat Genet** 48: 1024–1030

Saisho D, Ishii M, Hori K, Sato K (2011) Natural variation of barley vernalization requirements: Implication of quantitative variation of winter growth habit as an adaptive trait in east Asia. **Plant Cell Physiol** 52: 775–784

Sakuma S, Golan G, Guo Z, Ogawa T, Tagiri A, Sugimoto K, Bernhardt N, Brassac J, Mascher M, Hensel G, Ohnishi S, Jinno H, Yamashita Y, Ayalon I, Peleg Z, Schnurbusch T, Komatsuda T (2018) Unleashing floret fertility by a mutated homeobox gene improved grain yield during wheat evolution under domestication. **bioRxiv** 434985 doi: 10.1101/434985

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

Sánchez-León S, Gil-Humanes J, Ozuna Carmen V, Giménez María J, Sousa C, Voytas Daniel F, Barro F (2017) Low-gluten, nontransgenic wheat engineered with CRISPR/Cas9. **Plant Biotechnol J** 16: 902–910

Schmalenbach I, March TJ, Bringezu T, Waugh R, Pillen K (2011) High-resolution genotyping of wild barley introgression lines and fine-mapping of the threshability locus *thresh-1* using the Illumina GoldenGate assay. **G3-Genes Genom Genet** 1: 187–196

Scott JC, Manisterski J, Sela H, Ben-Yehuda P, Steffenson BJ (2014) Resistance of *Aegilops* species from Israel to widely virulent African and Israeli races of the wheat stem rust pathogen. **Plant Dis** 98: 1309–1320

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

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

Sorensen AE (1986) Seed dispersal by adhesion. **Annu Rev of Ecol Syst** 17: 443–463

Sourdille P, Cadalen T, Gay G, Gill B, Bernard M (2008) Molecular and physical mapping of genes affecting awning in wheat. **Plant Breed** 121: 320–324

Steffenson BJ, Olivera P, Roy JK, Jin Y, Smith KP, Muehlbauer GJ (2007) A walk on the wild side: Mining wild wheat and barley collections for rust resistance genes. **Aust J Agric Res** 58: 532–544

Stein JC, Yu Y, Copetti D, Zwickl DJ, Zhang L, Zhang C, Chougule K, Gao D, Iwata A, Goicoechea JL, Wei S, Wang J, Liao Y, Wang M, Jacquemin J, Becker C, Kudrna D, Zhang J, Londono CEM, Song X, Lee S, Sanchez P, Zuccolo A, Ammiraju JSS, Talag J, Danowitz A, Rivera LF, Gschwend AR, Noutsos C, Wu C-C, Kao S-M, Zeng J-W, Wei F-J, Zhao Q, Feng Q, El Baidouri M, Carpentier M-C, Lasserre E, Cooke R,

Rosa Farias D, da Maia LC, dos Santos RS, Nyberg KG, McNally KL, Mauleon R, Alexandrov N, Schmutz J, Flowers D, Fan C, Weigel D, Jena KK, Wicker T, Chen M, Han B, Henry R, Hsing Y-C, Kurata N, de Oliveira AC, Panaud O, Jackson SA, Machado CA, Sanderson MJ, Long M, Ware D, Wing RA (2018) Genomes of 13 domesticated and wild rice relatives highlight genetic conservation, turnover and innovation across the genus *Oryza*. **Nat Genet** 50: 285–296

Swanson-Wagner RA, Eichten SR, Kumari S, Tiffin P, Stein JC, Ware D, Springer NM (2010) Pervasive gene content variation and copy number variation in maize and its undomesticated progenitor. **Genome Res** 20: 1–11

Taenzler B, Esposti RF, Vaccino P, Brandolini A, Effgen S, Heun M, SchÄFer-Pregl R, Borghi B, Salamini F (2002) Molecular linkage map of Einkorn wheat: Mapping of storage-protein and soft-glume genes and bread-making quality QTLs. **Genet Res** 80: 131–143

Taketa S, Amano S, Tsujino Y, Sato T, Saisho D, Kakeda K, Nomura M, Suzuki T, Matsumoto T, Sato K, Kanamori H, Kawasaki S, Takeda K (2008) Barley grain with adhering hulls is controlled by an ERF family transcription factor gene regulating a lipid biosynthesis pathway. **Proc Natl Acad Sci USA** 105: 4062–4067

Tanksley SD, Nelson JC (1996) Advanced backcross QTL analysis: A method for the simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines. **Theor Appl Genet** 92: 191–203

Tiwari VK, Wang S, Sehgal S, Vrána J, Friebe B, Kubaláková M, Chhuneja P, Doležel J, Akhunov E, Kalia B, Sabir J, Gill BS (2014) SNP discovery for mapping alien introgressions in wheat. **BMC Genomics** 15: 273

Torada A, Amano Y (2002) Effect of seed coat color on seed dormancy in different environments. **Euphytica** 126: 99–105

Trevaskis B, Bagnall DJ, Ellis MH, Peacock WJ, Dennis ES (2003) MADS box genes control vernalization-induced flowering in cereals. **Proc Natl Acad Sci USA** 100: 13099–13104

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

Uauy C, Distelfeld A, Fahima T, Blechl A, Dubcovsky J (2006) A NAC gene regulating senescence improves grain protein, zinc, and iron content in wheat. **Science** 314: 1298

Varshney RK, Marcel TC, Ramsay L, Russell J, Röder MS, Stein N, Waugh R, Langridge P, Niks RE, Graner A (2007) A high density barley microsatellite consensus map with 775 SSR loci. **Theor Appl Genet** 114: 1091–1103

Vavilov NI, Freier F (1926) *Studies on The Origin of Cultivated Plants*. Trudi Po Prikl bot gen i Selek 16

Wang J, Luo MC, Chen Z, You FM, Wei Y, Zheng Y, Dvorak J (2013) *Aegilops tauschii* single nucleotide polymorphisms shed light on the origins of wheat D-genome genetic diversity and pinpoint the geographic origin of hexaploid wheat. **New Phytol** 198: 925–937

Wang S, Wong D, Forrest K, Allen A, Chao S, Huang BE, Maccaferri M, Salvi S, Milner SG, Cattivelli L, Mastrangelo AM, Whan A, Stephen S, Barker G, Wieseke R, Plieske J, International Wheat Genome Sequencing C, Lillemo M, Mather D, Appels R, Dolferus R, Brown-Guedira G, Korol A, Akhunova AR, Feuillet C, Salse J, Morgante M, Pozniak C, Luo M-C, Dvorak J, Morell M, Dubcovsky J, Ganal M, Tuberosa R, Lawley C, Mikoulitch I, Cavanagh C, Edwards KJ, Hayden M, Akhunov E (2014) Characterization of polyploid wheat genomic diversity using a high-density 90000 single nucleotide polymorphism array. **Plant Biotechnol J** 12: 787–796

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

Wendler N, Mascher M, Himmelbach A, Johnston P, Pickering R, Stein N (2015) Bulbosum to Go: A toolbox to utilize *Hordeum vulgare/bulbosum* introgressions for breeding and beyond. **Mol Plant** 8: 1507–1519

Wilhelm EP, Turner AS, Laurie DA (2009) Photoperiod insensitive *Ppd-A1a* mutations in tetraploid wheat (*Triticum durum* Desf.). **Theor Appl Genet** 118: 285–294

Winfield MO, Wilkinson PA, Allen AM, Barker GLA, Coghill JA, Burridge A, Hall A, Brenchley RC, D'Amore R, Hall N, Bevan MW, Richmond T, Gerhardt DJ, Jeddeloh JA, Edwards KJ (2012) Targeted re-sequencing of the allohexaploid wheat exome. **Plant Biotechnol J** 10: 733–742

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

Yan L, Loukoianov A, Blechl A, Tranquilli G, Ramakrishna W, San Miguel P, Bennetzen JL, Echenique V, Dubcovsky J (2004) The wheat *VRN2* gene is a flowering repressor down-regulated by vernalization. **Science** 303: 1640–1644

Yan L, Fu D, Li C, Blechl A, Tranquilli G, Bonafede M, Sanchez A, Valarik M, Yasuda S, Dubcovsky J (2006) The wheat and barley vernalization gene *VRN3* is an orthologue of *FT*. **Proc Natl Acad Sci USA** 103: 19581–19586

Yoshioka M, Iehisa JCM, Ohno R, Kimura T, Enoki H, Nishimura S, Nasuda S, Takumi S (2017) Three dominant awnless genes in common wheat: Fine mapping, interaction and contribution to diversity in awn shape and length. **PLoS ONE** 12: e0176148

Yu G, Champouret N, Steuernagel B, Olivera PD, Simmons J, Williams C, Johnson R, Moscou MJ, Hernández-Pinzón I, Green P, Sela H, Millet E, Jones JDG, Ward ER, Steffenson BJ, Wulff BBH (2017) Discovery and characterization of two new stem rust resistance genes in *Aegilops sharonensis*. **Theor Appl Genet** 130: 1207–1222

Yu J, Holland JB, McMullen MD, Buckler ES (2008) Genetic design and statistical power of nested association mapping in maize. **Genetics** 178: 539–551

Yuo T, Yamashita Y, Kanamori H, Matsumoto T, Lundqvist U, Sato K, Ichii M, Jobling SA, Taketa S (2012) A *SHORT INTERNODES* (*SHI*) family transcription factor gene regulates awn elongation and pistil morphology in barley. **J Exp Bot** 63: 5223–5232

Zakhrabekova S, Gough P, Braumann I, Müller AH, Lundqvist J, Ahmann K, Dockter C, Matyszczak I, Kurowska M, Druka A, Waugh R, Graner A, Stein N, Steuernagel B, Lundqvist U, Hansson M (2012) Induced mutations in circadian clock regulator *Mat-a* factilitated short-season adaptation and range extension in cultivated barley. **Proc Natl Acad Sci USA** 109: 4326–4331

Zhang Z, Belcram H, Gornicki P, Charles M, Just J, Huneau C, Magdelenat G, Couloux A, Samain S, Gill BS, Rasmussen JB, Barbe V, Faris JD, Chalhoub B (2011) Duplication and partitioning in evolution and function of homoeologous Q; loci governing domestication characters in polyploid wheat. **Proc Natl Acad Sci USA** 108: 18737–18742

Zhao G, Zou C, Li K, Wang K, Li T, Gao L, Zhang X, Wang H, Yang Z, Liu X, Jiang W, Mao L, Kong X, Jiao Y, Jia J (2017) The *Aegilops tauschii* genome reveals multiple impacts of transposons. **Nat Plants** 3: 946–955

Zhao Q, Feng Q, Lu H, Li Y, Wang A, Tian Q, Zhan Q, Lu Y, Zhang L, Huang T, Wang Y, Fan D, Zhao Y, Wang Z, Zhou C, Chen J, Zhu C, Li W, Weng Q, Xu Q, Wang ZX, Wei X, Han B, Huang X (2018) Pan-genome analysis highlights the extent of genomic variation in cultivated and wild rice. **Nat Genet** 50: 278–284

Zimin AV, Puiu D, Hall R, Kingan S, Clavijo BJ, Salzberg SL (2017a) The first near-complete assembly of the hexaploid bread wheat genome, *Triticum aestivum*. **GigaScience** 6: 1–7

Zimin AV, Puiu D, Luo MC, Zhu T, Koren S, Marçais G, Yorke JA, Dvořák J, Salzberg SL (2017b) Hybrid assembly of the large and highly repetitive genome of *Aegilops tauschii*, a progenitor of bread wheat, with the MaSuRCA mega-reads algorithm. **Genome Res** 27: 787–792

Zohary D (1959) Is *Hordeum agriocrithon* the ancestor of six-rowed cultivated barley? **Evolution** 13: 279–280

Zohary D, Hopf M, Weiss E (2012) Domestication of Plants in the Old World: The origin and spread of domesticated plants in Southwest Asia, Europe, and the Mediterranean Basin. Oxford University Press on Demand, Oxford, United Kingdom

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