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The Domestication Syndrome Genes Responsible for the Major Changes in Plant Form in the Triticeae Crops

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The process of crop domestication began 10,000 years ago in the transition of early humans from hunter/gatherers to pastoralists/farmers. Recent research has revealed the identity of some of the main genes responsible for domestication. Two of the major domestication events in barley were (i) the failure of the spike to disarticulate and (ii) the six-rowed spike. The former mutation increased grain yield by preventing grain loss after maturity, while the latter resulted in an up to 3-fold increase in yield potential. Here we provide an overview of the disarticulation systems and inflorescence characteristics, along with the genes underlying these traits, occurring in the Triticeae tribe.

Keywords: Barley • Domestication • Non-brittle rachis • Six-rowed spike • Triticeae • *vrs1*.

Abbreviations: HD-Zip, homoeodomain leucine zipper; QTL, quantitative trait locus.

Introduction

The domestication of a plant species refers to the various genetic modifications to a wild progenitor which have been selected as the plant form has been modified to meet human needs (Doebley et al. 2006). Studying domestication provides a glimpse of the history of the selection and improvement made by our forebears over several thousands of years in their transition from hunter/gatherer to pastoralist/farmer. A number of so-called 'domestication syndrome' plant traits are common to many of our crop species, in particular the loss of seed shattering, the minimization of seed dormancy and the increase in both seed size and number (Zohary and Hopf 2000), and their selection represented the first steps along the path to domestication and improvement.

The tribe Triticeae within the Pooideae subfamily of the grass family Poaceae includes the temperate cereals barley (*Hordeum vulgare* ssp. *vulgare* L.), bread and durum wheat (*Triticum aestivum* L. and *T. durum* Desf.), rye (*Secale cereale* L.) and the synthetic species triticale (×*Triticosecale* Wittm.), along with about 350 other species (Löve 1984). The majority of these species are wild, but some—particularly those belonging to the genera *Agropyron*, *Elymus*, *Leymus* and *Psathyrostachys*—are economically significant as perennial, fodder grasses (Kawahara 2009, Knüpffer 2009). The barley crop is grown mainly as grain for animal feed and as a source of malt for brewing, while the wheat crop is largely used as a source of flour for the production of baked goods or pasta. Together, wheat and barley dominate cereal production in Europe, North Africa, the Americas and parts of Asia (the largest and fifth largest acreage worldwide in the year 2009, http://www.fao.org.), and their domestication is closely interwoven with human history, because they represent the founder crops which built Western agriculture (Harlan 1971, Abbo et al. 2010).

The 31 species within the genus *Hordeum* consist of combinations of the four diploid genomes referred to as **H**, **I**, **Xa** and **Xu** (Bothmer et al. 1995, Blattner 2009). The size of the cultivated barley genome is at least 5.5 Gb (Smith and Flavell 1975, Wicker et al. 2009), or about 14 times that of the rice (*Oryza sativa* L.) genome (IRGSP 2005) and 45 times that of the *Arabidopsis thaliana* (L.) Heynh. genome (Arabidopsis Genome Initiative 2000). Its large size is a consequence of the large amount (some 80% of the genome) of highly repetitive gene-poor DNA (Bennett and Smith 1976, Bennett and Leitch 2005). Its closest wild relative is the annual, diploid and mainly inbreeding *spontaneum* barley (*H. vulgare* ssp. *spontaneum* C. Koch, **I** genome), held to be the direct progenitor of cultivated barley. There is no crossing barrier between *spontaneum* and cultivated barley (Bothmer et al. 1995). The distribution of *spontaneum* barley stretches from SE Europe and NE Africa, through the Near East (West Asia) to western Pakistan and southern Tajikistan (Bothmer et al. 1995). Natural stands can be found from sea level in the Mediterranean basin to 4,500 m a.s.l. in the Himalayas (Bothmer et al. 1995). Cultivated barley is grown throughout the temperate world.

A critical domestication trait in barley is the tough (non-brittle) rachis, since spikes of this type retain the grain beyond maturity, whereas in brittle types the spikes disintegrate at maturity, allowing the grain to fall to the ground.

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As a result, the early farmer would have tended to harvest grain from non-brittle spikes much more often than from brittle ones, thereby imposing a heavy selection pressure for the trait (Pourkheirandish and Komatsuda 2007). A second key domestication trait was the six-rowed spike, since this is able to set three times as many grains as the wild type two-rowed spike. In this review, we describe the state of knowledge regarding these two key barley domestication genes and discuss the potential applications of this knowledge in the wider context of crop improvement.

Spike architecture in the Triticeae

Inflorescence branching is dependent on the developmental fate of the axillary shoot meristem (Ward and Leyser 2004). The final architecture of the inflorescence is the end product of the number of meristems, their arrangement and their activity. In rice, sorghum, etc., it takes the form of a panicle, in wheat, barley, etc., a spike, while in maize, the male inflorescence forms as a panicle, but the female forms as a spike. It is thought that the panicle is the primitive form, from which the spike evolved at a later time (Vegetti and Anton 1995). The flowers of a grass plant develop on a specialized short branch called the spikelet (**Fig. 1**). This structure is the end result of an iterated branching process, and its final form depends on whether or not particular branch primordia grow, and by axis orientation in space (Doust and Kellogg 2002).

Spikelet numbers per node in the Triticeae are summarized in **Table 1**. Most species develop one spikelet per node, but, uniquely, the barley spike carries three, comprising one central and two lateral spikelets (**Fig. 1**). The central spikelet is fully fertile, but the two lateral spikelets are either staminate or completely sterile in two-rowed barley, while in six-rowed barley all three are fully fertile (Pourkheirandish and Komatsuda 2007). The three spikelets trait is rare enough to question how it evolved in the genus *Hordeum*. In bread wheat, supernumerary spikelets develop occasionally (Dobrovolskaya et al. 2009), and in the absence of the 2D chromosome a pair of spikelets commonly develops at the rachis node (Muramatsu 2009). In rye, a multispikelet mutation produces the so-called 'monstrosum' spike (Dobrovolskaya et al. 2009). Both the supernumerary spikelets trait in wheat and the 'monstrosum' spike in rye are under the control of a gene(s) mapping to the short arm of a homoeologous group 2 chromosome (Dobrovolskaya et al. 2009), suggesting the presence of a suppressor of the multispikelet trait on this chromosome arm. In the genus *Elymus*, the number of spikelets per rachis node can vary from one to two (paired), to even four, both along a single spike and between species within the genus (Muramatsu 2009). The numbers of spikelets per node may be controlled by the same gene on homoeologous group 2 in the tribe Triticeae. Inflorescence branching has also been observed and genetically dissected in *A. thaliana*. When the dosage of chromosome 5 increases to three, a number of abnormal phenotypes, including a 'triple branched flower' occur (Fig. 2, also see Henry et al. 2010). Although the causative gene(s) for this character have not been identified, some candidates have been proposed. These include *REVOLUTA*, which encodes a homoeodomain leucine zipper (HD-Zip) III protein, and is responsible for the development of apical meristems and for limiting cell division in the leaf and stem (Talbert et al. 1995).

In barley, the mutant *brc1* produces a branched spike (but not a change in the number of spikelets per rachis node), and

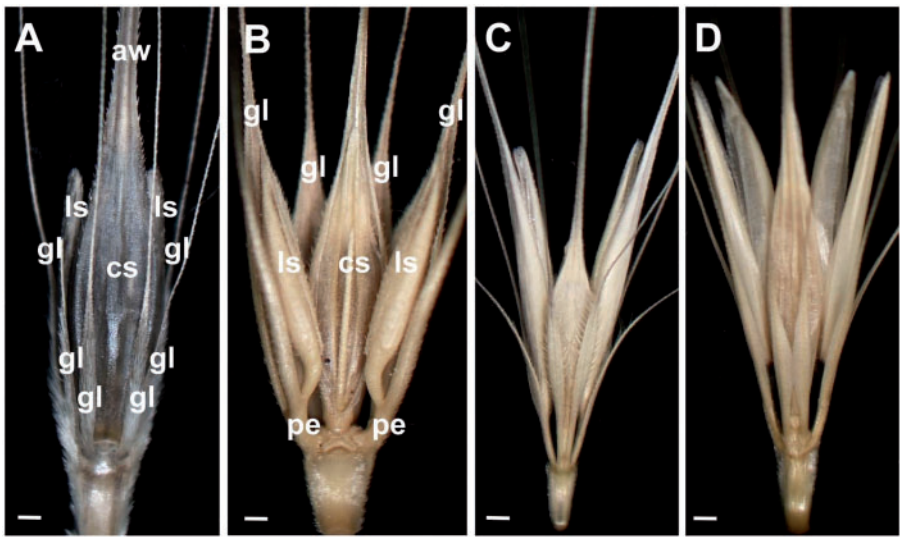

Fig. 1 Spike variation among wild *Hordeum* species. (A) *Spontaneum* barley develops a large central spikelet and two small lateral ones. (B) The large glumes of *H. pusillum* are the same size as its lemma. (C) In *H. murinum*, the two lateral spikelets are larger than the awned central spikelet. (D) In *H. bulbosum*, the lateral spikelets are larger than the unawned central one. cs, central spikelet; ls, lateral spikelet; gl, glume; pe, pedicel; aw, awn. Scale bar = 1 mm.

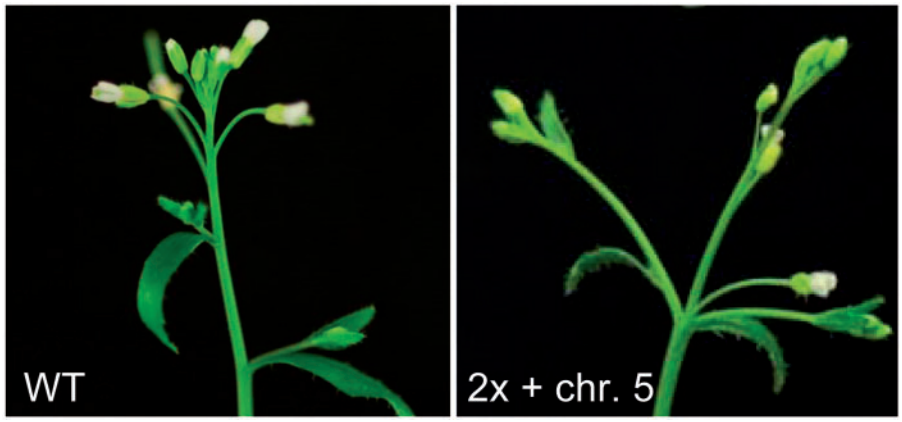

Fig. 2 The triple-branched flower produced by *A. thaliana* ecotype Columbia-0 plants trisomic for chromosome 5 (right, by courtesy of Dr. Isabelle Henry) and a normal flower produced by wild-type diploid plants (left, by courtesy of Dr. Hiroaki Ichikawa).

the causative gene maps to chromosome 2HS (Rossini et al. 2006); a likely ortholog is *FRIZZY PANICLE* of rice (Komatsu et al. 2003), while in maize three *RAMOSA* genes have been implicated in the control of tassel branching (Vollbrecht et al. 2005). One of these (*ra1*) maps to chromosome 7 in a region syntenous with barley chromosome 2H, and encodes a Cys_2-His_2 zinc-finger protein, a member of a family of plant-specific EPF subclass transcription factors (Vollbrecht et al. 2005). The second gene (*ra2*) maps to chromosome 3 and encodes a lateral organ boundary domain transcription factor (Bortiri et al. 2006). The pattern of expression of *ra2* homologs appears to be well conserved among rice, barley, sorghum and maize, suggesting that its role is important for the initial determination of inflorescence architecture. Finally, *ra3* maps to chromosome 7 and encodes a trehalose-6-phosphate phosphatase (Satoh-Nagasawa et al. 2006). *ra3* is transcriptionally regulated by *ra1*.

Evolution of the barley six-rowed spike

Six-rowed barley produces three times as many seeds per spike as the two-rowed type, and the restoration of fertility of the two lateral spikelets has been viewed as a domestication syndrome trait (Komatsuda et al. 2007). The oldest known archaeological barley kernels date from about 19,000 years ago, and were certainly derived from two-rowed, brittle rachis types (Zohary and Hopf 2000). The earliest domesticated barley samples were unearthed in Jarmo (northern Iraq), date to 8,400–9,500 years ago and were derived from two-rowed, non-brittle types. Six-rowed types first make an appearance at Tell Abu Hureyra (Syria), dating to 8,000–8,800 years ago. Following the development of agriculture in the alluvial soils of Mesopotamia and, later in Lower Egypt (6,000–7,000 years ago), the six-rowed spike began largely to replace the two-rowed type, and established itself as the most important crop in the Near East (Helbaek 1959, Zohary and Hopf 2000).

All *spontaneum* barleys are two rowed, which is an advantageous trait for a wild species, since the arrowhead shape of the spikelet at maturity helps it to become buried in the soil once it disarticulates (Bothmer et al. 1995); in addition, the degenerating pair of lateral spikelets form a hook-like structure, which allows its ready attachment to an animal coat, and thus promotes seed dispersal. The success of this structure can be seen by the much wider geographical distribution of *spontaneum* barley compared with that of diploid *Triticum* species, which develop only a single spikelet per node (Bothmer et al. 1995).

The genetic basis of the six-rowed spike in barley has been fully elucidated (Komatsuda et al. 2007). The trait is expressed in the presence of the recessive *vrs1* allele at the *six-rowed spike 1* locus mapping to chromosome 2HL. *vrs1* has been isolated by positional cloning, and its functional allele (*HvHox1*) has been shown to encode a HD-Zip type I transcription factor (Komatsuda et al. 2007). The gene is thought likely to have arisen following the duplication of its ancestral gene *HvHox2*, a HD-Zip I transcription factor, mapping to chromosome 2HS (Sakuma et al. 2010).

The function of HD-Zip transcription factors

The HD-Zip family of transcription factors, which is unique to the plant kingdom, features a leucine zipper (Zip) motif lying immediately downstream of the homoeodomain (HD). HD-Zip genes have been isolated from *A. thaliana*, rice, sunflower, barley, etc. The HD is responsible for the specificity of DNA binding. HD-Zip proteins bind as dimers to DNA, and the absence of Zip abolishes their binding ability (Sessa et al. 1993). HD-Zip proteins have been classified into four subfamilies (I–IV) on the basis of a set of diagnostic features, additional common motifs and physiological functions (Sessa et al. 1993). HD-Zip I genes have evolved, through a series of gene duplications, into a number of paralogous subsets, in which the genes share a common intron/exon structure (Ariel et al. 2007, Sakuma et al. 2010). Several members of the HD-Zip I and II families have been associated with auxin signaling and transport (Kawahara et al. 1995, Morelli and Ruberti 2002), as well as

with light signaling responses (Carabelli et al. 1993, Steindler et al. 1999, Wang et al. 2003) and de-etiolation (Aoyama et al. 1995). A number of HD-Zip I and II genes are involved in the regulation of adaptation to drought (Lee et al. 2001, Manavella et al. 2006). While HD-Zip I and II proteins interact with similar pseudo-palindromic binding sites (Sessa et al. 1993, Meijer et al. 1997), slightly different sequences are recognized by the HD-Zip III and IV proteins (Sessa et al. 1998, Abe et al. 2003, Ohashi et al. 2003, Nakamura et al. 2006). The genes in these two latter categories share the conserved START domain (Ponting and Aravind 1999). HD-Zip III genes have been shown to be involved in the regulation of apical embryo patterning, embryonic shoot meristem formation, organ polarity, vascular development and meristem function (Ratcliffe et al. 2000, McConnell et al. 2001, Green et al. 2005, Prigge et al. 2005, Byrne 2006). HD-Zip IV genes appear to be involved in the determination of cell fate in the epidermis and in the regulation of cell layer-specific expression (Ito et al. 2002, Yang et al. 2002, Abe et al. 2003, Nakamura et al. 2006).

The function of *Vrs1*

The expression of *Vrs1* is strictly limited to the two lateral spikelet primordia in the immature two-rowed barley spike, which is consistent with the idea that the VRS1 protein acts to suppress development of the two lateral spikelets. Loss of *Vrs1* function converts the rudimentary lateral spikelets seen in the two-rowed barley spike into fully fertile spikelets. The *Vrs1* gene showed the first clear biological function of HD-Zip I type transcription factors in plant. Resequencing of the *HvHox1* sequence across a large sample of both *spontaneum* and cultivated accessions has confirmed the association between the HvHOX1 peptide sequence and spike type (Saisho et al. 2009), and has indicated that six-rowed barley probably arose at least four times (Komatsuda et al. 2007, Saisho et al. 2009). The *deficiens* type (which develops rudimentary lateral spikelets) sequence is defined by a serine to glycine mutation at position 184 of motif 3, lying outside the HD-Zip sequence proper, indicating that the HD-Zip domain is not the sole determinant for the development of the lateral spikelets. Reverse genetics using Targeting Local Lesions IN Genomes (TILLING) was successful in the detection of new mutant alleles, and analogous mutational events were detected (Gottwald et al. 2009).

The spike of most wild *Hordeum* species is two rowed, although there is variation with respect to the size of the glume, awn and pedicel. In some species, e.g. *H. bulbosum* L. (**I** genome) and *H. murinum* L. (**Xu** genome), the lateral spikelets are larger than the central one, even though they remain sterile (**Fig. 1**). Apart from in cultivated barley, the six-rowed spike is found only in *H. bogdanii* Wilensky (**H** genome, **Fig. 3D**, and Bothmer et al. 1995), but the genetic basis of the trait in this species has not as yet been determined. It is assumed that primitive farmers preferred *H. vulgare* to *H. bogdanii*, because they appreciated the former's larger seed size, lesser dormancy and perhaps its better taste. *Vrs1* orthologs are present in all wild *Hordeum* species tested to date (unpublished data), although their function in these species remains to be investigated.

The evolution of *HvHox1*

DNA duplication is a major player in genome evolution (Ohno 1970, Zhang 2003). In some cases, a duplicated gene acquires a new function while the ancestral copy retains its original function; but, in other cases, one or other duplicate is lost over evolutionary time (Kellogg and Bennetzen 2004, Devos 2005, Bennetzen 2007). *Vrs1* and *HvHox2* both consist of three exons and two introns, and their gene products share many residues; but their expression profiles are very distinct. The question is as

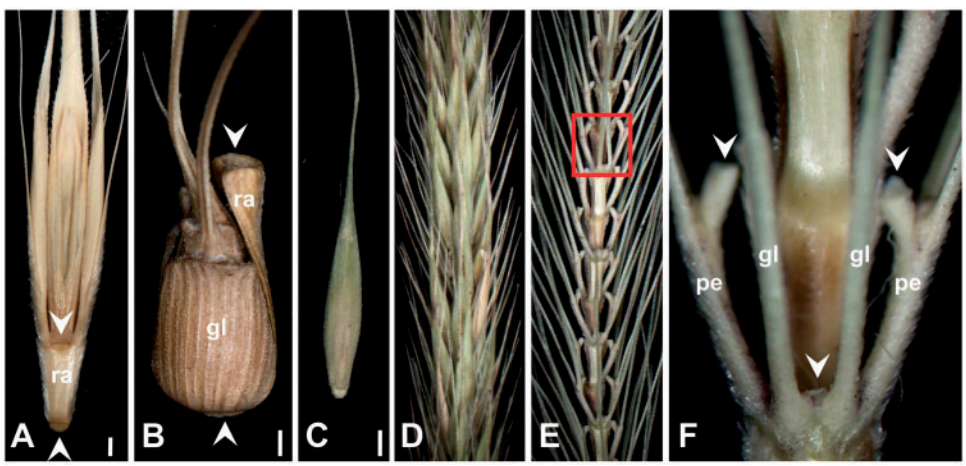

Fig. 3 The disarticulation system of *Triticeae*. (A) A wedge-type spikelet of *H. vulgare* ssp. *spontaneum* var. *proskowetzii* Nábelek. (B) A barrel-type spikelet of *Ae. tauschii*. (C) A glume-type spikelet of *H. bogdanii*. (D) Spike architecture of *H. bogdanii*, showing three fertile spikelets per rachis node. (E) The disarticulation of the spike above the glume in *H. bogdanii*. (F) A close-up of the region marked by the red box in (E). Arrowheads show the point of disarticulation. ra, rachis; gl, glume; pe, pedicel. Scale bar = 1 mm.

to how *Vrs1* acquired its modern function. *Vrs1* expression is strictly limited to the lateral spikelets of the immature spike (Komatsuda et al. 2007), whereas *HvHox2* expression is ubiquitous (Sakuma et al. 2010). However, their level of expression in the spike may be rather similar. The VRS1 and HvHOX2 sequences differ in their homoeodomain and, in addition, the former has lost the C-terminal motif. The homoeodomain mutation could create a changed DNA binding affinity, and the absence of the C-terminal motif may serve to decrease the level of its interaction with transcription activators—although it has not been established as yet whether either HvHOX2 or VRS1 operate as transcriptional repressors or activators. Based on the hypothesis that HvHOX2 and VRS1 share the same target DNA sequence and retain the same level of affinity, we have proposed that VRS1 competes with HvHOX2 to bind to a *cis*-element(s) within a downstream gene(s). A result of the simultaneous expression of *Vrs1* and *HvHox2* is that the formation of HvHOX2–VRS1 heterodimers would drive down the population of HvHOX2 homodimers present, so that the stronger the expression of *Vrs1*, the greater the degree of *HvHox2* suppression (**Fig. 4**).

Disarticulation systems in the Triticeae

Disarticulation, or the disintegration of the spike at maturity, has evolved in nature to aid seed dispersal. In wild Triticeae species, the spike breaks either at its lowest node, at the rachis nodes or above the glumes within the rachilla; these various disarticulation points generate, as dispersal units, whole spikes, spikelets and individual grains, respectively. 'Wedge-type' spikelets are formed when disarticulation occurs immediately above the rachis node, while 'barrel-type' spikelets are formed when the breakage occurs below the rachis node (**Fig. 3**, and Zohary and Hopf 2000). The pattern of spike disarticulation among the Triticeae species is summarized in **Table 1**. Genera producing whole spikes (disarticulation at its lowest node) are rare, and there is roughly a 50–50 split between those producing a brittle rachis and those where disarticulation occurs above the glume. The genera *Hordeum* and *Eremopyrum* are exceptional for including species of both these types. All the *Hordeum* species, except for *H. bogdanii* Wilensky, disarticulate above the rachis node, to produce wedge-type spikelets (**Fig. 3**, and Bothmer 1979). Three *Eremopyrum* species disarticulate above the rachis node, and one disarticulates above the glume (Frederiksen 1991b).

In rice, a clear abscission layer is formed above the glume (Konishi et al. 2006, Li et al. 2006), but there is little or no convincing histochemical demonstration of the existence of an abscission layer above the glume in any Triticeae species. Abscission occurs in each junction between the florets within the spikelet of many Triticeae genera (**Table 1**). As a result, it has been proposed that abscission above the glume is the ancestral form of disarticulation present in the common progenitor of rice, the Triticeae species and species within the genera *Avena*, *Bromus* and *Brachypodium* (Ladizinsky and Zohary 1971, Opanowicz et al. 2008). According to this notion, therefore, the

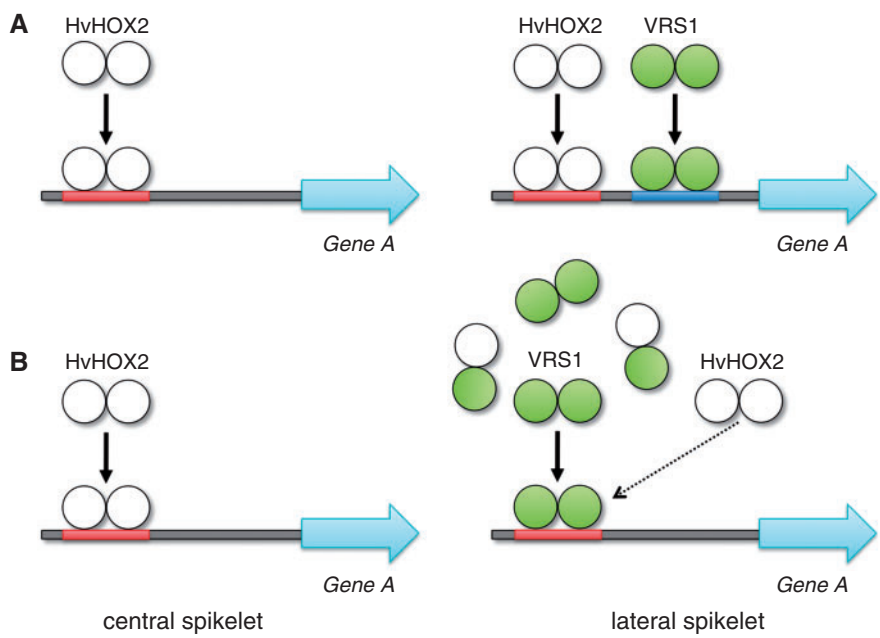

Fig. 4 Two alternative hypotheses for the interaction of *HvHox2* and *Vrs1*. (A) In the central spikelet, only *HvHox2* is expressed, thus allowing the HvHOX2 homodimer (white) to bind to its downstream target. In the lateral spikelets, both *HvHox2* and *Vrs1* are expressed, but the VRS1 (green) and HvHOX2 proteins bind to different downstream targets. (B) VRS1 targets the same DNA sequence as HvHOX2, thus allowing for competition between VRS1 and HvHOX2. The formation of HvHOX2–VRS1 heterodimers (white/green) drives down the number of HvHOX2 homodimers produced, so that the stronger the expression of *Vrs1*, the greater the degree of the *HvHox2* suppression.

Table 1 Morphological characterization in Triticeae

Genus	Genome symbol	No. of spikelets per node	No.of florets per spikelet	References	Whole spike, disarticulation at lowest node	Brittle rachis, disarticulation		Tough rachis, disarticulation		References
Agropyron	**P**	1	>2	Frederiksen and Seberg (1992)					Above glume	Melderis (1980a)
Heteranthelium	**Q**	1	>2	Frederiksen and Seberg (1992)			Above node			Frederiksen (1993)
Crithopsis	**K**	2	2	Frederiksen and Seberg (1992)			Above node			Frederiksen (1993)
Taeniatherum	**Ta**	2	1 or 2	Frederiksen and Seberg (1992)			Above node			Frederiksen (1986), this study
Hordelymus	**Ns**	2–3	1	Mizianty et al. (2007), Barkworth and Bothmer (2009)					Above glume	Humphries (1980), this study
Festucopsis	**L**	1	>2	Frederiksen and Seberg (1992)					Above glume	Barkworth and Bothmer (2009)
Australopyrum	**W**	1	>2	Frederiksen and Seberg (1992)					Above glume	Connor (1994)
Pseudoroegneria	**St**	1	>2	Frederiksen and Seberg (1992), Jarvie and Barkworth (1992)					Above glume	Barkworth and Bothmer (2009)
Elymus	**St, H, Y, P, W**	1–4	>2	Frederiksen and Seberg (1992), Sun and Salomon (2009)	Lowest node[a]				Above glume	Melderis (1980b)
Elytrigia	**St, E, P**	1	>2	Jarvie and Barkworth (1992), Barkworth and Bothmer (2009)				Below glume[b]	Above glume	Salomon and Lu (1994)
Thinopyrum	**E**	1	>2	Frederiksen and Seberg (1992), Jarvie and Barkworth (1992)			Above node			Barkworth and Bothmer (2009)
Lophopyrum	**E**	1	>2	Frederiksen and Seberg (1992), Jarvie and Barkworth (1992)					Above glume	This study
Trichopyrum	**ESt**, **EESt**[c]	1	>2	Jarvie and Barkworth (1992), this study					Above glume	This study
Psammopyrum	**EStP**, **ELP**	1	>2	This study					Above glume	This study
Roegneria	**StY**	1	>2	Yang and Zhou (1994), Barkworth and Bothmer (2009)					Above glume	Barkworth and Bothmer (2009)
Psathyrostachys	**Ns**	2–3	1 or 2	Frederiksen and Seberg (1992)			Above node			Baden (1991)
Leymus	**NsXm**	1–5	>2	Barkworth and Atkins (1984), Barkworth and Bothmer (2009)					Above glume	Melderis (1980c)
Pascopyrum	**StHNsXm**	1	>2	Barkworth and Bothmer (2009)					Above glume	Barkworth and Bothmer (2009)
Amblyopyrum	**T**	1	>2	Frederiksen and Seberg (1992)			Above node			Kimber and Feldman (1987), van Slageren (1994)
Hordeum	**H, Xa, Xu, I**	3	1	Frederiksen and Seberg (1992)			Above node		Above glume	Bothmer et al. (1979, 1995)
Aegilops	**S, C, D, M, N, U, X**	1	>2	Frederiksen and Seberg (1992)	Lowest node	Below node	Above node			van Slageren (1994)

(continued)

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Table 1 Continued

Genus	Genome symbol	No. of spikelets per node	No.of florets per spikelet	References	Whole spike, disarticulation at lowest node	Brittle rachis, disarticulation		Tough rachis, disarticulation		References
Triticum	**A**, **AB**, **AAB**, **ABD**	1	>2	Frederiksen and Seberg (1992)	Lowest node	Below node	Above node			Kimber and Feldman (1987)
Secale	**R**	1	2	Frederiksen and Seberg (1992)			Above node			Frederiksen and Petersen (1998)
Dasypyrum	**V**	1	>2	Frederiksen and Seberg (1992)			Above node			Frederiksen (1991a), this study
Eremopyrum	**FXe**	1	>2	Frederiksen and Seberg (1992)			Above node		Above glume	Frederiksen (1991b)
Henrardia	**O**	1	1 or 2	Frederiksen and Seberg (1992)		Below node				Frederiksen (1993)
Kengyilia	**StYP**	1	>2	Barkworth and Bothmer (2009)					Above glume	Barkworth and Bothmer (2009)
Peridictyon	**Xp**	1	>2	Frederiksen and Seberg (1992)					Above glume	Barkworth and Bothmer (2009)
Eremium	**N**	1–2	1–3	Seberg and LindeLaursen (1996), Barkworth and Bothmer (2009)					Above glume	Barkworth and Bothmer (2009)
Stenostachys	**HW**	1–3	1–3	Connor (1994), Barkworth and Bothmer (2009)					Above glume	Connor (1994)
Hystrix	**StH**, **Ns**	2 to many	1 or 2	Baden et al. (1997), Barkworth and Bothmer (2009)					Between florets (this plant has no glume)	Hitchcock (1950), this study
Sitanion	**StH**	≥2	2–3	Wilson (1963), Barkworth and Bothmer (2009)			Above node			Hitchcock (1950), this study

[a] *Elymus humidus* disarticulates the whole spike.
[b] *Elytrigia repens* disariculates below the glume.
[c] Wang et al. (1994).

brittle rachis, as well as the whole spike disarticulation type, is a derived form unique to the Triticeae, all of which produce a spike type of inflorescence. The recognition of an abscission layer has been difficult in the genera *Hordeum*, *Triticum* and *Aegilops*, although a correlation has been drawn between rachis fragility and the depth of the constriction around the rachis node (Von Ubisch 1915, Matsumoto et al. 1963).

Genetics of the non-brittle rachis in barley

In *spontaneum* barley, the disarticulation scars are smooth, whereas in cultivated barley mechanical threshing produces a rough scar on grains detached from the rachis. This feature has served as a diagnostic of domesticated barley in archaeological grain samples (Zohary and Hopf 2000). The domestication of barley occurred between 8,400 and 9,500 years ago. In *spontaneum* barley, the brittle rachis is specified by the two complementary dominant genes *Btr1* and *Btr2* (Takahashi and Hayashi 1964), which are tightly linked with one another on the short arm of chromosome 3H (Takahashi and Hayashi 1964, Komatsuda and Mano 2002). However, in cultivated barley, one or the other of these genes has been lost by mutation during domestication, so that most European/West Asian cultivars are of genotype *btr1Btr2*, while most East Asian ones are *Btr1btr2* (Takahashi 1955).

In addition, a further two quantitative trait loci (QTLs) have been detected on chromosomes 5H and 7H (Komatsuda and Mano 2002, Komatsuda et al. 2004). The latter ('D') has a stronger effect in conjunction with the main complementary pair. 'D' maps close to the *dense spike 1* (*dsp1*) locus, which specifies the length of the spike internode. This has been taken to suggest the possibility that the 'D' effect is due to the pleiotropic action of *dsp1* rather than to the action of an independent gene. The semi-brachytic mutation *uzu* also produces a dense spike, but it is unclear whether the presence of this gene has any (Komatsuda et al. 2004) or much (Senthil and Komatsuda 2005) effect on the brittleness of the rachis. The wild-type alleles at each of these genes is dominant, i.e. the non-brittle rachis is determined by a loss-of-function allele. None of these non-brittle rachis genes, however, has proven to be allelic to the 'head shattering' QTL mapped to chromosome 3H by Kandemir et al. (2000). The former was located on the long arm of chromosome 5H (Komatsuda et al. 2004) and, due to the location on the homeologous region, the QTL could be a homolog of the wheat free-threshing gene Q (Simons et al. 2006). The Q gene encodes a member of the AP2 class transcription factors and the *q* allele produces speltoid spikes, in which the disarticulation pattern was such that the rachis broke to form wedge-type spikelets.

In rice, the *qSH1* (*QTL of seed shattering in chromosome 1*), which produces an abscission layer above the glume, encodes a BEL1-type homoeobox gene (Konishi et al. 2006), while *sh4* (*QTL 4 responsible for the reduction of grain shattering*), which produces an identical phenotype, encodes a Myb3 transcription factor (Li et al. 2006). The genetic location of *qSH1* on rice chromosome 1 is within a region syntenous with barley chromosome 3H (Stein et al. 2007). The barley *qSH1* ortholog *JuBel2* maps to barley chromosome 3HL (Muller et al. 2001), while the *btr1* and *btr2* loci reside on 3HS (Komatsuda and Mano 2002), thereby excluding the possibility that *JuBel2* is a candidate for either *btr1* or *btr2*. Komatsuda et al. (2004) have made a start towards the map-based cloning of *btr1* and *btr2* by constructing a high-density amplified fragment length polymorphism (AFLP)-based genetic map of the region; at present the position of *btr1* has been defined to an interval of 0.8 cM (Azhacuvel et al. 2006).

Based on the phenotype of single chromosome addition lines into bread wheat, brittle rachis genes have been located on various Triticeae species homoeologous group 3 chromosomes (Watanabe and Ikebata 2000), including *Dasypyrum villosum* (L.) Candargy (DV) chromosome 3VS (Urbano et al. 1988), *Thinopyrum bessarabicum* (Savul. & Rayss) Löve chromosome $3E^b$ (King et al. 1997), *Aegilops bicornis* (Forssk.) Jaub. & Spach chromosome $3S^b$ (Riley et al. 1966, Chapman and Miller 1979; both cited in Urbano et al. 1988) and *Ae. sharonensis* Eig chromosome $3S^l$ (Miller 1983; cited in Urbano et al. 1988). All of these chromosomes carry a gene(s) responsible for disarticulation above the rachis node. In *Ae. longissima* Schweinf. & Muschl., a 'fragile rachis' trait is also under the control of a gene(s) on the short arm of chromosome $3S^l$, but its disarticulation type has not been clearly described (Ceoloni 1983). Within *Triticum* itself, the above rachis node disarticulation gene(s) have been located on a Tibetan bread wheat chromosome 3DS (Chen et al. 1998), *Triticum timopheevi* Zhuk. chromosome 3AS (Li and Gill 2006) and *Triticum turgidum* L. ssp. *dicoccoides* (Korn. ex Asch. and Graebner) Thell. chromosome 3AS and 3BS (Nalam et al. 2006). Whole spike type disarticulation in *Ae. uniaristata* Vis. is due to a gene(s) on chromosome 3N (Miller et al. 1995) and in *Ae. speltoides* Tausch on chromosome 3SS (Li and Gill 2006). Thus there are grounds for supposing that the disarticulation genes as a whole form an orthologous set, and just differ from one another by the topology of their expression—either above each rachis node, or solely at the base of the spike. Intriguingly, in *Ae. tauschii* Coss., the progenitor species of the bread wheat D genome, the below the rachis node disarticulation trait (**Fig. 3B**) is controlled by a gene(s) mapping to the long arm of chromosome 3D (Li and Gill 2006). Nevertheless, this gene too may still belong to the same orthologous set, because the intrachromosomal transposition of genes is a far from rare event during evolution (Tarchini et al. 2000, Li and Gill 2002, Ilic et al. 2003, Pourkheirandish et al. 2007, Faris et al. 2008, Sakuma et al. 2010).

Future research

Most domestication genes responsible for the major morphological change in cereal crops are transcriptional regulators, suggesting that this class of genes played a central role during

domestication (Doebley et al. 2006, Gross and Olsen 2010). The barley six-rowed spike was caused by a loss-of-function mutation of the HD-Zip I transcription factor (Komatsuda et al. 2007), indicating that this gene controls cell division and development specifically in the lateral spikelets. The *Vrs1* orthologs of wheat, *Brachypodium*, rice, sorghum and maize were absent, indicating that this transcription factor is specific to barley (Sakuma et al. 2010). In the case of the loss of seed shattering which is a classical domestication trait, responsible loci are conserved in Triticeae, but the rice shattering is controlled by different loci. These findings indicate that there are multiple genetic pathways to modify the domestication traits because of the existence of various species-specific transcription factors. The structural downstream gene controlled by a specific transcription factor might be conserved throughout the species. Thus, our next target should be the downstream genes of transcription factors in order to understand the mechanism of regulation of domestication genes. In the case of the six-rowed spike, there would be three approaches to elucidating the regulation mechanism: (i) protein interaction; (ii) microarray; and (iii) genetic approaches. In the first approach, chromatin immunoprecipitation (ChIP) of transcription factors followed by sequencing (ChIP-SEQ) is a powerful method (Kaufmann et al. 2010) to investigate the hypothesis that VRS1 and HvHOX2 proteins are targeted to the same or a different DNA-binding site (*cis*-element of a downstream gene). Yeast two-hybrid analysis would be effective to unravel the hypothesis of whether VRS1 and HvHOX2 proteins make heterodimers or not (Ohashi-Ito et al. 2002). In the second approach, we would test the microarray using the mutant which lacks the *Vrs1* segment in order to understand the gene(s) that moves on the same network as *Vrs1*. In the last approach, it is possible to use the six-rowed spike mutant lines induced from two-rowed spike parents which are independent loci (*vrs2*, *vrs3*, *vrs4* and *vrs5*) of *vrs1* (Lundqvist et al. 1997, Pourkheirandish and Komatsuda 2007). It is possible that these responsible genes establish the regulatory network for the development of the lateral spikelets.

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