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Using genetics to advance breeding: The winter barley example

P.M. Hayes*, J.S. Skinner**, T.H.H. Chen** and P. Szűc*
*Department of Crop and Soil Science, Oregon State University, Corvallis, OR 97331, USA
**Department of Horticulture, Oregon State University, Corvallis, OR 97331, USA

SUMMARY – The winter hardiness of cereal crops is associated with low temperature tolerance, vernalization (the requirement of exposure to an extended period of low temperature), and photoperiod sensitivity. Understanding the genetics of these traits, using agronomically relevant germplasm, will provide new opportunities for sustainable and productive barley production. Using a new generation of germplasm and massively parallel data sets we are anticipating new insights into the ancestral and derived conditions of barley.

The winter hardiness of cereal crops is associated with the requirement of exposure to an extended period of low temperature (vernalization) in order to achieve a timely transition from vegetative to reproductive growth. Understanding the genetics of vernalization is a prerequisite to improving winterhardiness and improved winterhardiness will allow for more sustainable and productive cereal crop production in the face of global warming.

The classification of growth habit in barley (Hordeum vulgare subsp. vulgare) is based on vernalization requirement and can be described as winter, facultative, or spring. Vernalization requirement in barley is not absolute – an unvernalized winter genotype will eventually flower under favorable growth conditions. However, the flowering is so delayed as to be agronomically unacceptable (Karsai et al., 2001). Technically speaking, winter barley genotypes do not "require" vernalization – since they will eventually flower. It may be more appropriate to say they are very "responsive", or "sensitive" to vernalization in that the number of days elapsed from planting to flowering will be substantially reduced if plants receive a vernalization treatment.

The genetic basis of vernalization response/sensitivity in barley was first described, based on phenotypic data, in terms of a three-locus epistatic model (Takahashi and Yasuda 1971). Using current nomenclature and chromosome designations, the loci are VRN-H1 (5H), VRN-H2 (4H) and VRN-H3 (1H). Winter genotypes have the allelic architecture Vrn-H2/vrn-H1/vrn-H3/vrn-H3. All other allelic configurations lead to a lack of significant vernalization response, e.g. spring and facultative growth habit. There is no allelic variation at VRN-H3 in most cultivated genotypes, reducing the genetic model to two factors (Yasuda et al., 1993).

HvBM5A, a MADS-box floral meristem identity gene, is considered to be the determinant of VRN-H1 (Dany luk et al., 2003; Trevaskis et al., 2003; von Zitzewitz et al., 2005; Yan et al., 2003). In wheat and barley, allelic variation at VRN-1 is ascribed to mutations in the promoter and/or first intron (Yan et al., 2003; Yan et al., 2004; a von Zitzewitz et al., 2005). The key regulatory region in the intron has been narrowed down to a highly conserved 0.44-kb segment "critical region" (Fu et al., 2005; von Zitzewitz et al., 2005).

A zinc finger CCT domain transcription factor (ZCCT), which is a flowering repressor down-regulated by vernalization, is the candidate for wheat and barley VRN-2 (Yan et al., 2004b). Allelic variation at this locus is ascribed to loss-of-function mutations or complete deletion leading to recessive spring growth habit (Dubcovsky et al., 2005; Karsai et al., 2005; von Zitzewitz et al., 2005; Yan et al., 2004b). There are three tightly linked ZCCT genes in barley (ZCCT-Ha, ZCCT-Hb and ZCCT-Hc) and two in diploid wheat (ZCCT-1 and ZCCT-2) (Dubcovsky et al., 2005; Karsai et al., 2005; Yan et al., 2004b). In wheat and barley, ZCCT-1 and ZCCT-Ha (respectively) were reported to be are the most likely candidates for VRN-2 (Dubcovsky et al., 2005; Yan et al., 2004b). However, Trevaskis et al. (2006) and Yan et al. (2004b) have shown that during vernalization under long-day conditions, the expression of ZCCT-Hb and the two wheat ZCCT genes are down-regulated.
There is evidence that the photoperiod and vernalization sensitivity pathways that culminate in flowering are connected. High levels of barley and wheat ZCCT expression were detected only when photoperiod-responsive plants were grown under long-day conditions (Dubcovsky et al., 2006; Trevaskis et al., 2006). These results provide a molecular basis for explaining quantitative trait locus (QTL) associations of VRN-H2 with photoperiod sensitivity (Karsai et al., 2005; Karsai et al., 2006; Laurie et al., 1995; Szücs et al., 2006). In photoperiod-responsive wheat and barley plants grown under short-day conditions (at either cold or room temperature) ZCCT expression was repressed, but there was no increase in VRN-1 expression. This suggests the presence of at least one other VRN-1 repressor (Dubcovsky et al., 2006; Trevaskis et al., 2006). A candidate gene is VRT-2, a putative flowering repressor MADS-box gene regulated by both vernalization and day length; this gene shows higher expression under short-day (vs long-day) in a photoperiod-sensitive barley (Kane et al., 2005). HvVRT-2 is on the short arm of chromosome 7H and is associated with photoperiod sensitivity QTL (Szücs et al., 2006).

The two-locus epistatic model for VRN gene interaction is supported by extensive phenotypic data in wheat and barley populations segregating for growth habit (Dubcovsky et al., 2005; Dubcovsky et al., 2006; Fu et al., 2005; Karsai et al., 2005; Kóti et al., 2006; Laurie et al., 1995; Takahashi and Yasuda 1971; Tranquilli and Dubcovsky 2000; Yan et al., 2003; Yan et al., 2004a; Yan et al., 2004b). A molecular model explaining the VRN-2/VRN-1 epistatic interaction in winter cereals was proposed by Yan et al. (2003; 2004a; 2004b). According to this model, VRN-2 encodes a dominant repressor which inhibits the expression of VRN-1. Vernalization down-regulates Vrn-2 expression, allowing expression of vrn-1 alleles in winter habit genotypes. No or little vernalization sensitivity is observed in genotypes with recessive vrn-2 alleles (loss-of-function mutations or complete deletions of ZCCT), regardless of the allelic state at VRN-1. Likewise, genotypes with a dominant Vrn-2 allele but with a dominant Vrn-1 allele (lacking a repressor binding site in the promoter and/or in the intron 1) will show minimal vernalization sensitivity.

We have genetically validated the VRN-H2/VRN-H1 epistatic model under long-day conditions, using allele sequence and flowering time phenotypic data from segregating barley populations. The uniqueness of this approach is that the three parental accessions are all spring habit but based on allele sequencing we determined that each genotype has a winter type allele at either the VRN-H1 or the VRN-H2 locus. We predicted that we would observe vernalization sensitivity (delayed flowering in the absence of vernalization) in a subset of segregating progeny of specific crosses. Dicktoo has a winter (vrn-H1) HvBM5A allele but has a deletion of all three ZCCT-H genes and is therefore homozygous vrn-H2. This particular allele configuration defines the facultative growth habit (sensu von Zitzewitz et al., 2005). The Oregon Wolfe Barley Dominant genetic stock has a spring (Vrn-H1) HvBM5A allele due to a large deletion of the intron 1. All three ZCCT-H genes are present in this accession, making it Vrn-H2. (Fu et al., 2005). In an extensive screen of barley germplasm with VRN-H1- and VRN-H2-specific primers, we found that the ZCCT-H genes and the 436 bp vernalization critical region of HvBM5A intron 1 are present in the spring habit accession Calicuchima-sib (I. Karsai, personal communication). We therefore made three crosses: Dicktoo × Oregon Wolfe Barley Dominant; Dicktoo × Calicuchima-sib, and Calicuchima-sib × Oregon Wolfe Barley Dominant. We hypothesized that we would observe vernalization sensitivity in the progeny of Dicktoo (vrn-H2/ vrn-H1/vrn-H1/vrn-H1) × Oregon Wolfe Barley Dominant (Vrm-H2/Vrm-H2/Vrm-H1/Vrn-H1) cross. The crosses with Calicuchima-sib were designed to determine if this accession is an exception to the two-locus model or if it has novel "spring" alleles at VRN-H1 and/or VRN-H2.

The results of this research validate the two-locus epistatic model for vernalization and provide a predictive tool for germplasm screening and selection. We have discovered winter alleles in exotic and adapted spring barley varieties of interest for their human nutritional properties. Targeted crosses among such lines, followed by marker assisted selection in their progeny, should expedite the development of winter habit barley varieties with unique quality profiles.

References


Karsai, I., Mészáros, K., Szűcs, P., Hayes, P.M., Láng, L. and Bedő, Z. (2006). The Vrn-H2 locus (4H) is influenced by photoperiod and is a major determinat of plant development and reproductive fitness traits in a facultative × winter barley (*Hordeum vulgare* L.) mapping population. *Plant Breed. DOI.*


