Wheat gene for all seasons

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Diverse seasonal flowering behaviors drive global adaption of bread wheat (*Triticum aestivum*), the major crop grown in temperate zones worldwide. Many wheats are sown in autumn and flower only after experiencing the prolonged cold of winter (vernalization). By delaying flowering until spring, the requirement for vernalization minimizes the risk that frost-sensitive flowers and developing grain will be damaged by freezing. This flowering behavior is important in regions where crops are sown in autumn and experience cold winters. In other regions, warm climates, or where crops are sown in spring, the need for cold to stimulate flowering limits wheat cultivation. To adapt wheats to these regions, genes that reduce the vernalization requirement have been used to breed varieties that flower without vernalization. Previous studies have identified the sequences of three of these genes: *VERNALIZATION1* (*VRN1*), *VRN2*, and *VRN3* (1–5). In PNAS, Kippes et al. (6) identify the gene sequence of *VRN4*, a fourth gene controlling the vernalization requirement of wheat. The authors show that *VRN4* is a translocated copy of the *VRN1* gene.

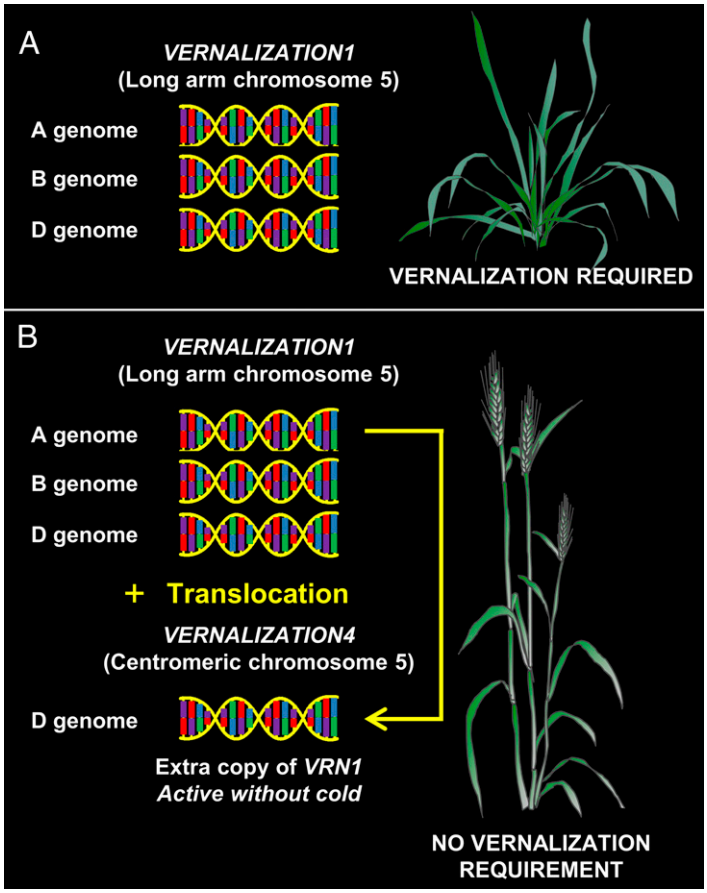

Fig. 1. Origin of the wheat *VRN4* gene that reduces the vernalization requirement. (*A*) Ancestral hexaploid genome of bread wheat (*T. aestivum*) had three homeologous *VRN1* genes, one on the long arm of chromosome 5 for each of the A, B, and D genomes. *VRN1* is a promoter of flowering, but the *VRN1* genes are not transcribed until plants experience prolonged cold (vernalization), so flowering is delayed. In this figure, the haploid equivalent is shown, and, normally, there are six copies per nucleus (i.e., AABBDD). (*B*) *VRN1* gene translocated from the long arm of chromosome 5 (A genome) to the centromeric region of chromosome 5 (D genome, proximal region of short arm). The additional *VRN1* gene on chromosome 5D has increased transcriptional activity and triggers flowering without vernalization. This extra copy of the *VRN1* gene is the basis for the *VRN4* gene.

VRN1 encodes a MADS box (MCM1/AGAMOUS/DEFICIENS/SRF) transcription factor (1–3). In vernalization-requiring "winter wheats," *VRN1* is transcriptionally activated by prolonged cold to trigger flowering. "Spring wheats" that flower without vernalization typically carry alleles of *VRN1* that are actively transcribed without cold, which reduce or eliminate the requirement for vernalization. Kippes et al. (6) show that *VRN4* is a variation on this theme: an additional copy of *VRN1* that is transcribed without prior cold treatment (Fig. 1). A loss-of-function mutation in the extra copy of *VRN1* restores the vernalization requirement, demonstrating that this additional copy of *VRN1* corresponds to the *VRN4* gene (6). *VRN4* occurs widely in an ancient South Asian wheat subspecies, *T. aestivum ssp. sphaerococcum*, where the extra copy of *VRN1* might have originated (6). The reason why the extra copy of *VRN1* is active without prior cold exposure is not clear. One possibility is that mutations in the extra copy of *VRN1* disrupt the binding site of a RNA binding repressor protein (7). Another possibility is that the new chromosomal location might influence transcriptional activity of the translocated gene copy. Further studies are needed to resolve these possibilities.

The study by Kippes et al. (6) further highlights the importance of *VRN1* as a regulator of vernalization and as a major gene controlling adaptation and life cycle strategies of wheat. A range of different alleles of *VRN1* have been identified in cereal breeding programs (8). It seems likely that further diversity in *VRN1* awaits characterization and that this diversity can be harnessed for wheat breeding. Screening for direct regulatory targets of *VRN1* has provided insights into a broader genetic network controlling flowering in wheat (9). Similarly, transcriptional regulation of *VRN1* activity has been investigated (10–12). There is now great potential to investigate how *VRN1* is activated by the cold

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of winter, which is the key to understanding the molecular basis for the vernalization response in cereals. Perhaps the most basic questions are how cereals sense cold and measure the passage of time during winter. The study of Kippes et al. (6) suggests one avenue to investigate these questions: RNA processing pathways.

The discovery that *VRN4* is an additional copy of *VRN1* raises interesting questions about how natural variation has been harnessed to breed modern wheat cultivars. For example, why is activation of *VRN1* the major mechanism for reducing the vernalization requirement in bread wheat? Part of the answer is that bread wheat is a hexaploid crop, and recessive genes that reduce the vernalization requirement are less likely to be deployed. Another explanation is that alternative genes that reduce the vernalization requirement might compromise other important traits (e.g., grain yield), and so are not used in wheat breeding. A final explanation is that active alleles of *VRN1* (and *VRN4*) might have been common in wild wheats at the dawn of agriculture, and so were easily incorporated into cultivated varieties (13). The vernalization requirement is an important trait, so it will be worthwhile to explore other ways to breed wheats that flower without vernalization. Efforts to map other vernalization genes will be of great interest (14).

The findings of the study by Kippes et al. (6) will have an impact on crop improvement. The identification of the *VRN4* gene sequence extends the complement of "perfect markers" for wheat vernalization genes. These markers can be used for marker-assisted selection in breeding populations. Perfect markers are also useful for parent selection, allowing wheat breeders to minimize the genetic complexity of polyploid traits in breeding crosses. Marker information for *VRN1* (and other genes) is already being used by breeders in this manner. *VRN4* might also allow breeders to avoid ancestral linkage relationships, such as between *VRN1* and other genes controlling flowering, for example (15), because *VRN4* is located at a new chromosomal address.

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A final perspective on the study by Kippes et al. (6) is that it provides an excellent example of current progress in crop genomics. The grand challenge for crop genomics is to harness ever-increasing sequence information to predict crop performance under field conditions. The past decade has seen rapid advances toward this objective, and our understanding of genes controlling the vernalization requirement in wheat is a leading example. More broadly, knowledge of genes controlling flowering behavior of wheat has progressed to the point where it will soon be possible to predict crop heading dates at different locations and sowing dates based on genotype data and climate information, with a high degree of accuracy. This ability to predict flowering dates will impact both crop improvement and crop management.

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