The molecular basis of vernalization-induced flowering in cereals

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Genetic analyses have identified three genes that control the vernalization requirement in wheat and barley; *VRN1*, *VRN2* and *FT* (*VRN3*). These genes have now been isolated and shown to regulate not only the vernalization response but also the promotion of flowering by long days. *VRN1* is induced by vernalization and accelerates the transition to reproductive development at the shoot apex. *FT* is induced by long days and further accelerates reproductive apex development. *VRN2*, a floral repressor, integrates vernalization and day-length responses by repressing *FT* until plants are vernalized. A comparison of flowering time pathways in cereals and *Arabidopsis* shows that the vernalization response is controlled by different MADS box genes, but integration of vernalization and long-day responses occurs through similar mechanisms.

Vernalization promotes flowering in cereals

Wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*) are grown in temperate regions throughout the world and account for approximately a third of total world grain production. Flowering of these cereals can be accelerated by prolonged exposure to cold – vernalization. Vernalization occurs during winter when temperatures are between 0° and 10 °C [1,2]. A few weeks of cold are often sufficient to promote flowering, but longer periods can accelerate flowering to a greater extent, up to the point when the vernalization response becomes saturated. This can require more than six weeks of vernalization [1,2]. Varieties that require vernalization are sown in late summer or autumn, are vernalized during winter and then flower in spring. There are also varieties of both wheat and barley that do not require vernalization to flower. These can be sown at different times of year and are also grown in regions where winter temperatures are not suitable for vernalization.

Three genes control the vernalization requirement

Genetic analyses in barley have shown that three genes determine the vernalization requirement; *VRN1*, *VRN2* and *VRN3* [1]. These same genes also determine the vernalization requirement in wheat [3–5]. *VRN1* has been isolated by map-based cloning in the diploid wheat progenitor *Triticum monococcum* [6], and independently in bread wheat on the basis of gene expression patterns [7,8].

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VRN2 has been identified by positional cloning [9], and *VRN3* has been mapped to a known gene; the cereal orthologue of the *Arabidopsis* (*Arabidopsis thaliana*) *FLOWERING LOCUS T* (*FT*) gene [5]. Molecular genetic analyses have revealed specific roles for *VRN1*, *VRN2* and *FT* in the vernalization or day-length response pathways. In this review, we describe the functions of *VRN1*, *VRN2* and *FT*, and examine how these genes regulate flowering.

VRN1 is induced by vernalization and promotes the transition to reproductive development

Vernalization accelerates flowering by promoting the switch from vegetative to reproductive development [2,10]. This transition is controlled by genes that regulate the identity of the shoot apical meristem to determine which organs are produced by the shoot apex [11]. During vegetative development the shoot apical meristem produces leaf primordia (Figure 1a,b). At the beginning of reproductive development the shoot apex acquires inflorescence meristem identity, and secondary meristems, known as floral primordia, begin to develop above each of the leaf primordia. This results in the appearance of distinctive double ridges on the side of the shoot apex, the first visible signs of reproductive development (Figure 1c). Subsequently the development of leaf primordia stops, and the floral primordia develop into the floral structures of the inflorescence [12] (Figure 1d–g). We will refer to the developmental stage marked by the appearance of double ridges as inflorescence initiation.

Vernalization accelerates inflorescence initiation by inducing the *VRN1* gene, a promoter of inflorescence meristem identity [6–8]. *VRN1* encodes an *APETALA1*-like MADS box transcription factor (*FRUITFULL* is the most closely related *AP1*-like gene in *Arabidopsis* [13]), a class of MADS box gene that regulates meristem identity in a range of plants. In varieties that require vernalization to flower, *VRN1* is initially expressed at low levels and is significantly induced by vernalization [6–8,14]. The extent to which *VRN1* is induced depends on the length of vernalization treatment [6,7,14,15], resulting in a quantitative effect on the timing of inflorescence initiation.

In varieties that flower without vernalization, expression of *VRN1* increases during inflorescence initiation and remains high through subsequent stages of apex development [16]. This suggests that *VRN1* has a role in regulating meristem identity that is not limited to the vernalization
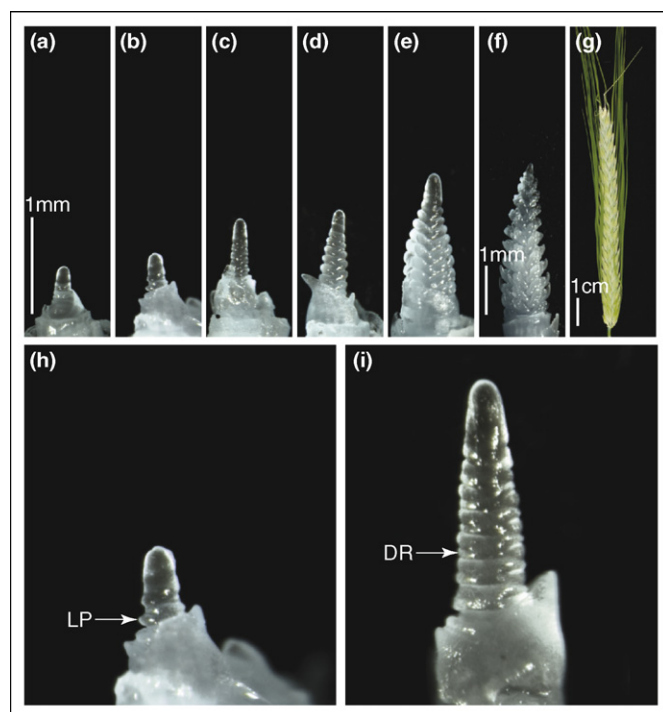
Figure 1. Phases of cereal shoot apex development. The shoot apex of barley develops vegetatively and produces leaf primordia (a,b) until inflorescence initiation occurs (c). At this point, floral primordia appear above the leaf primordia, giving rise to distinctive double ridges along the side of the shoot apex. The floral primordia then differentiate into the floral organs that give rise to the florets (d–g). Anthesis occurs around the time of head emergence (g). Higher magnification images show the morphological differences between a vegetative shoot apex (h) and a reproductive shoot apex (i). The leaf primordia (LP) and double ridges (DR) are indicated by arrows.

response. Expression of *VRN1* is probably required to establish and then maintain inflorescence meristem identity during reproductive shoot apex development.

FT accelerates flowering in long days

Flowering of barley and wheat can be accelerated by long days. Day-lengths above a threshold, typically more than 10 h, are required to accelerate flowering. Longer day-lengths promote flowering to a greater extent, up to a limit, typically between 13 and 18 h, beyond which there is no further effect on flowering time [17]. Long days accelerate flowering by accelerating reproductive apex development [10,17].

The day-length response is mediated by *FT*. *FT* encodes a polyethanolamine binding protein (PEBP) [18,19], a class of protein involved in cellular signalling in other organisms [20,21]. In *Arabidopsis*, *FT* expression increases in leaves when plants are exposed to inductive day-lengths (long days) [18,19] and the FT protein is transported to the shoot apex to promote flowering [22]. Similarly, in rice, *FT* expression is induced by inductive day-lengths (short days) [23,24] and the FT protein is transported from the leaf to the shoot apex to trigger flowering [25]. In wheat and barley, expression of *FT* is induced by long days and promotes flowering [26]. This probably involves transport of the *FT* protein from the leaf to the shoot apex.

In barley, long-day induction of *FT* requires the *PHOTOPERIOD1* gene (*PPD-H1*), and varieties with an inactive version of *PPD-H1* show reduced sensitivity to long days [26]. *PPD-H1* is a pseudo-response regulator gene, which encodes a pseudo-receiver domain, involved in signal transduction, and a CCT (CONSTANS, CONSTANS-like and TOC1) domain [26]. CCT domains interact with CCAAT box binding factors [27,28] and occur in proteins that regulate circadian rhythm or day-length responses. *PPD-H1* is expressed with a diurnal pattern and might moderate day-length induction of *FT* by controlling *CONSTANS* (*CO*) activity [26].

VRN2 is a floral repressor that integrates the vernalization and day-length responses

Some day-length sensitive varieties have a strong requirement for vernalization, which is a pre-requisite for long-day induction of flowering [1,17]. In field conditions, crops sown in late summer or autumn are insensitive to long days and grow vegetatively until vernalized during winter. Following winter, plants are able to respond to long days, which accelerate reproductive apex development as days lengthen in spring (Figure 2).

VRN2 is a floral repressor that delays flowering until plants are vernalized. *VRN2* encodes a protein with a zinc-finger motif, which might mediate DNA binding, and a CCT domain [9]. *VRN2* is expressed with a diurnal pattern in long days, but is not expressed in short days [29,30]. On the basis of this expression pattern, and the nature of the protein encoded by *VRN2*, we suggest that the primary role of *VRN2* is to block flowering in long-days by repressing *FT*. This could occur through direct interaction between the VRN2 protein and the *FT* gene sequence, or indirectly through interactions with other components of the photoperiod pathway, such as *PPD-H1*.

VRN2 expression decreases when plants are vernalized under long days, whereas expression of *VRN1* increases. On the basis of these reciprocal gene expression patterns it has been suggested that *VRN2* is repressed by low temperatures, allowing *VRN1* to increase [9]. Experimental evidence suggests this might not be the case. *VRN1* expression has been shown to repress expression of *VRN2* in both wheat and barley [29,31], so it is more likely that the decrease in *VRN2* expression seen when plants are vernalized in long days is caused by induction of *VRN1*. Regardless, vernalization under long days does not reflect field conditions, where vernalization occurs during the short days of winter. When plants are vernalized in short days, *VRN2* expression is low and is not affected by vernalization [29]. Thus, it is unlikely that *VRN2* plays a role in the vernalization response during winter.

In vernalization-requiring varieties, *VRN1*, *VRN2* and *FT* interact to promote spring flowering

We propose that regulatory interactions between *VRN1*, *VRN2* and *FT* integrate vernalization and long-day responses. Plants sown in late summer or autumn do not flower before winter because both the vernalization and day-length response pathways are inactive; *VRN1* expression is low and *VRN2* activity represses long-day induction of *FT*. Low temperatures during winter slow shoot apex development and induce expression of *VRN1*. As temperatures rise
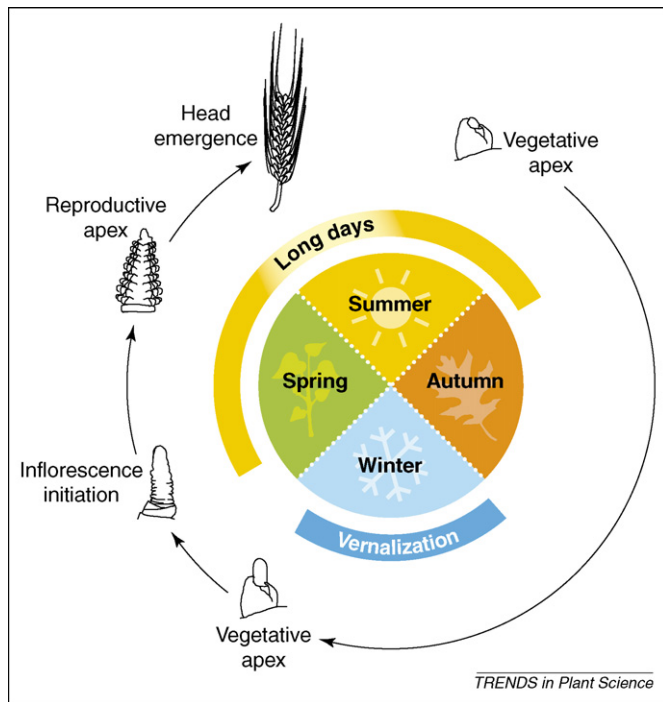
Figure 2. The influence of seasonal cues on shoot apex development in the temperate cereals. Varieties that require vernalization are sown in late summer or autumn. The shoot apex develops vegetatively until winter, when vernalization occurs. This promotes inflorescence initiation, which occurs as temperatures increase in spring. Long days in spring promote subsequent stages of reproductive apex development; head emergence occurs in late spring or early summer.

Figure 3. Molecular basis of vernalization-induced flowering in cereals versus *Arabidopsis*. In the temperate cereals (top), *VRN2* represses *FT* and blocks long-day promotion of flowering before winter. *VRN2* is not expressed in the short days of winter, when *VRN1* is induced by prolonged exposure to cold. After winter, *VRN1* expression remains high. This promotes inflorescence initiation and represses *VRN2*, to allow long-day induction of *FT* to accelerate reproductive development. When flowering occurs, *VRN1* expression is reset to establish the vernalization requirement in the next generation. In *Arabidopsis* (bottom), *FLC* is expressed before winter and represses *FT*. Vernalization represses *FLC*, and this allows long-day induction of *FT* (and *SOC1*) to promote flowering in spring. *FLC* expression is reset during meiosis to establish the vernalization requirement in the next generation.

towards the end of winter, the rate of apex development increases, and *VRN1* promotes inflorescence initiation, which can occur during late winter or early spring. *VRN1* also represses *VRN2*. This allows long-day induction of *FT*, which accelerates reproductive development after winter. Inflorescence initiation can occur while day-lengths remain relatively short, so although induction of *FT* might accelerate inflorescence initiation it might also be important to accelerate subsequent stages of reproductive development that are sensitive to day-length in cereals [17]. Flowering (anthesis and head emergence) then occurs in late spring or early summer (Figure 3).

High basal levels of *VRN1* expression can substitute for vernalization

Alleles of *VRN1* that have high basal levels of *VRN1* expression can substitute for vernalization [6–8]. These alleles accelerate inflorescence initiation and are dominant to alleles that are expressed only after vernalization [1,3]. Alleles of *VRN1* that have high basal expression levels also repress *VRN2* [29,31]. This might allow long days to induce expression of *FT* and further accelerate floral development in day-length-sensitive varieties. There are a range of dominant alleles of *VRN1* with different levels of activity, and the extent to which such alleles promote flowering is proportional to their basal level of *VRN1* expression [8]. The alleles of *VRN1* that are expressed without requirement for vernalization have mutations in the promoter or deletions within the first intron of the *VRN1* gene [6,32–34], suggesting that these regions are crucial for repression of *VRN1* before vernalization.
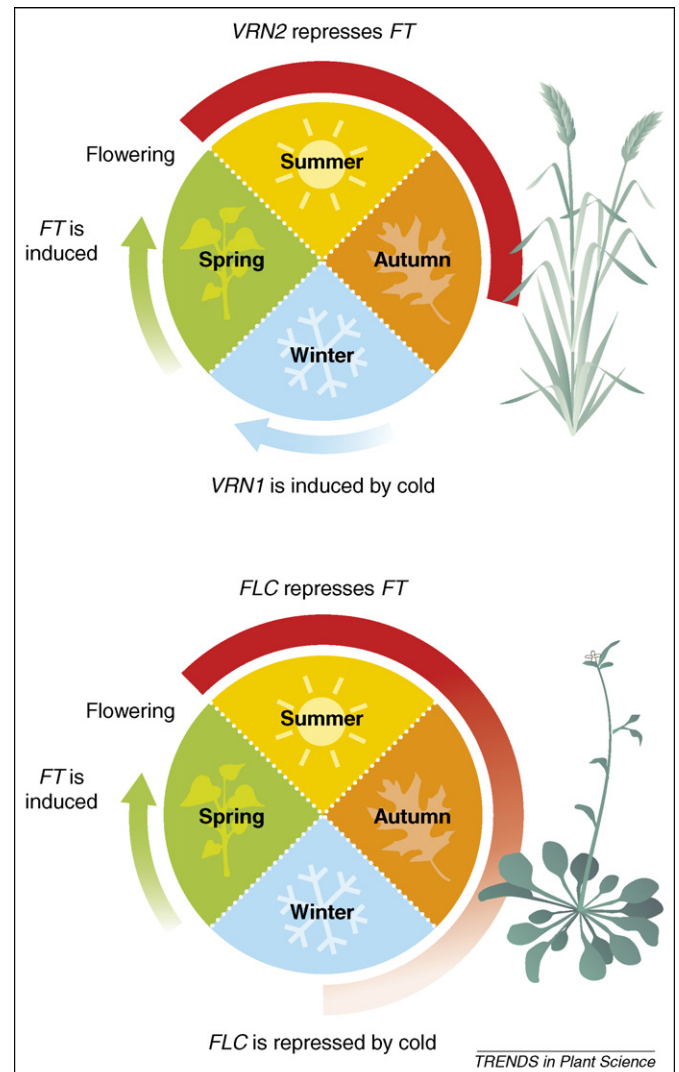
Activation of the day-length response can overcome the vernalization requirement

Varieties of wheat or barley that lack a functional copy of *VRN2* do not require vernalization to flower [1,9]. In *T. monococcum*, non-functional *VRN2* alleles have a mutation that causes an amino acid substitution at a conserved arginine in the CCT domain [9]. In barley, there are naturally occurring deletions of *VRN2* [9,35]. These cause early flowering in long days, but not in short-days [36], consistent with the suggestion that *VRN2* acts to block the promotion of flowering by long days [29]. *FT* is expressed at higher levels in lines that lack *VRN2* [5]. Thus, it seems likely that in the absence of *VRN2* activity, long-day induction of *FT* causes early flowering, which overcomes the requirement for vernalization. Although *VRN2* is required

to maintain the vernalization requirement, it is not crucial to the vernalization response. When barley varieties that lack *VRN2* are maintained in short-day conditions (where the day-length pathway remains inactive), vernalization can still induce *VRN1* [7,16] and accelerate flowering [36].

There are alleles of *FT* (*VRN3*) that are expressed without vernalization [5]. These bypass the requirement for a level of *VRN1* activity to allow a long-day flowering response. In barley, these alleles of *FT* have polymorphisms in the first intron [5]. In wheat (*T. aestivum*), there is a retroelement insertion in the promoter of *FT* [5]. These regions in the promoter or first intron of the *FT* gene are presumably important for repression of *FT* before vernalization, and might contain binding sites for the VRN2 protein [5]. Alleles of the barley *FT* gene that are expressed without vernalization still respond to long days, suggesting that the mutations in the intron found in these alleles do not prevent day-length regulation of *FT* [5].

In varieties that lack *VRN2*, or that have alleles of *FT* that are expressed without vernalization, *VRN1* is expressed at higher levels than in varieties that require vernalization. This might be caused by developmental induction of *VRN1* as the shoot apex develops toward inflorescence initiation, when *VRN1* activity is likely to be required to specify inflorescence meristem identity [16,29].

The molecular basis of spring flowering in *Arabidopsis*

Vernalization promotes spring flowering in many ecotypes of *Arabidopsis*. The central regulator of vernalization-induced flowering in *Arabidopsis* is a MADS box transcription factor gene, *FLOWERING LOCUS C* (*FLC*) [37,38]. *FLC* is a floral repressor that delays both the transition to reproductive apex development and long-day promotion of flowering until plants have experienced vernalization [37,38].

FLC represses transcription of two floral promoters; *FT* and *SUPPRESSOR OF OVER-EXPRESSION OF CONSTANS 1* (*SOC1*), a MADS box transcription factor that promotes the transition to reproductive apex development [39,40]. In plants that have not experienced vernalization, *FLC* is expressed at high levels [37,38], and the FLC protein binds to sequences in an intron of *FT* and the promoter of *SOC1* to repress transcription of both these genes [41]. This delays flowering.

Vernalization represses transcription of *FLC* [37,38]. This allows *FT* to be induced by long days, which promotes the transition to reproductive development and triggers flowering in spring (Figure 3). The degree to which *FLC* is repressed is proportional to the duration of cold exposure, allowing quantitative changes in flowering time in response to different lengths of vernalization [42]. Repression of *FLC* ceases around the time of meiosis, allowing the vernalization response to be reset in the next generation [42].

In naturally occurring ecotypes of *Arabidopsis*, there is a strong correlation between the level of *FLC* expression and vernalization requirement. Mutations in *FLC* [43,44] or in a second gene required for *FLC* expression, *FRIGIDA* [45], account for most natural variation in vernalization requirement in *Arabidopsis*.

Integration of vernalization and day-length responses occurs by a similar mechanism in *Arabidopsis* and cereals

The day-length response pathway is conserved in *Arabidopsis* and cereals: in both the monocot and dicot plants, *CO* up-regulates *FT* in inductive day-lengths to promote flowering [18,19,22–25]. The mechanism that integrates vernalization status and day-length responses is also similar; vernalization is required to allow long-day induction of *FT* (Figure 4). In *Arabidopsis* a single gene, *FLC*, represses *FT* to establish the vernalization requirement, and is down-regulated by prolonged cold to mediate the vernalization response. In the temperate cereals, two genes fulfil these roles; *VRN2* represses *FT* before winter to establish the vernalization requirement, and *VRN1* is induced by prolonged cold to mediate the vernalization response (Figure 4). No orthologues of *VRN2* have been identified outside the temperate cereals, so *VRN2* might have evolved as an integrator of vernalization status and long-day response during the evolution of grasses.

Do conserved epigenetic mechanisms regulate the vernalization response in *Arabidopsis* and cereals?

In *Arabidopsis*, transcriptional repression of *FLC* by vernalization is mediated by protein complexes that chemically modify histones [46,47]. These deacetylate or methylate specific residues of histones at the *FLC* locus, and presumably trigger conformational changes in chromatin
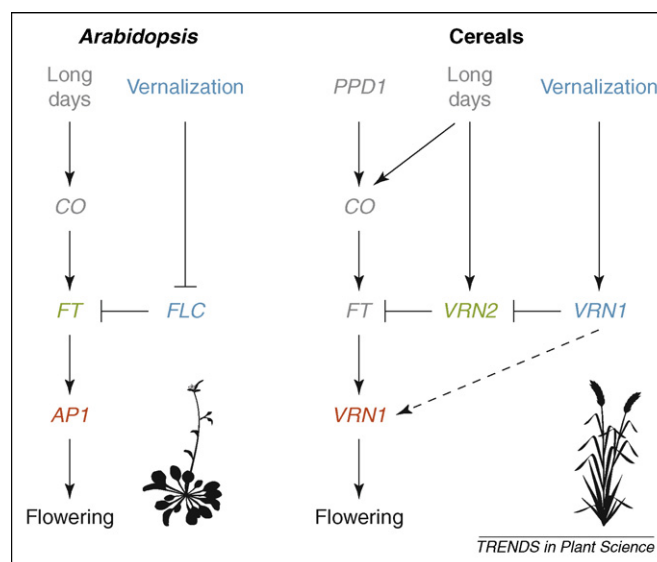

Figure 4. A comparison of the molecular pathways regulating flowering time in *Arabidopsis* and the temperate cereals. Vernalization and long days promote flowering in *Arabidopsis* (left) and in the temperate cereals (right). The day-length response is conserved (grey). *CONSTANS* (*CO*) senses long days and activates *FLOWERING LOCUS T* (*FT*) expression. This requires *PHOTOPERIOD1* (*PPD1*) in cereals. Vernalization is a prerequisite for long-day induction of *FT* in both *Arabidopsis* and cereals, but the vernalization pathway (blue) has evolved independently. In *Arabidopsis*, *FLOWERING LOCUS C* (*FLC*) blocks long-day induction of *FT* but is repressed by vernalization. In the temperate cereals, *VRN2* blocks long-day induction of *FT* before winter, but *VRN1* is induced by vernalization to repress *VRN2* and allow long-day induction of *FT*. In *Arabidopsis*, the vernalization and day-length response pathways intersect at *FT*, which can be described as a floral integrator gene (green). In cereals, *VRN2* is a floral integrator gene. In both *Arabidopsis* and the temperate cereals, activation of flowering causes expression of genes that promote inflorescence meristem identity (red), such as *APETALLA1* (*AP1*) in *Arabidopsis*. *VRN1* acts as both a flowering time gene in the vernalization response pathway (blue) and as a meristem identity gene during reproductive development (red).

structure that limit access of transcriptional machinery to the *FLC* gene [46,47]. Histones bound to regions of the first intron of *FLC* are targets for histone deacetylation and histone methylation [46–49], and these regions are required for repression [50]. Histone modifications at the *FLC* locus are mitotically stable and are maintained through the life cycle of the plant [46,47]. This epigenetic regulation of *FLC* activity provides the molecular basis for the somatic memory of vernalization in *Arabidopsis*, which can be reset every generation. The *VERNALIZATION INSENSITIVE 3* (*VIN3*) gene is required for repression of *FLC* by vernalization [46]. *VIN3* encodes a protein that is induced by cold and interacts with the histone modification complexes that repress *FLC* [51]. VIN3 might be involved in sensing cold [44].

The vernalization response in cereals could involve epigenetic regulation of *VRN1*. Vernalization has a cumulative effect on the transcriptional activity of *VRN1*, which is reset in the subsequent generation, and, as in *FLC*, there are regions in the first intron of *VRN1* that are required for transcriptional repression. These regions might be targeted by histone modification complexes similar to those that repress *FLC*. If so, this could provide the mechanism for a somatic memory of vernalization in cereals. Modifications of histones at the *VRN1* locus could cause mitotically stable repression of *VRN1* until plants have been vernalized, and then vernalization would activate protein complexes that reverse these modifications to activate *VRN1* expression. Chromatin would then be restored to the repressed state at meiosis to reset the vernalization response in the next generation.

Conclusions

The cloning of *VRN1*, *VRN2* and *FT* has facilitated progress in understanding how flowering is regulated by vernalization and day-length in cereals. Further investigation of the function of these genes, using reverse genetics or reporter gene constructs in transgenic plants, should offer further insights into how flowering time is controlled in cereals. It will be possible to examine whether *VRN1* is subject to epigenetic regulation during vernalization, and how *VRN1* interacts with *VRN2* to control the activity of the day-length response pathway.

The gene sequences of *VRN1*, *VRN2* and *FT*, as well as *PPD-H1*, should be useful to cereal breeding programs. Novel genetic variation in these important flowering-time genes can be rapidly identified by screening for differences in DNA sequence, and molecular markers for these genes can be used to simplify the breeding process. An increased understanding of how these genes interact to control flowering time should also improve predictions of how different environmental factors are likely to affect flowering time in different genetic backgrounds. This will be important for the development of varieties of these major food crops that are able to cope with climate change.

Update

Faure *et al*. [52] have recently described the expression patterns and chromosomal locations of four other barley *FT*-like genes and Shitsukawa *et al*. [53] have described mutant wheat that lacks *VRN1* and does not flower.

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Plant Science Conferences in 2007

21st Asian Pacific Weed Science Society Conference
2–6 October 2007
Colombo, Sri Lanka
http://www.apwss21.lk/

XVI International Plant Protection Congress
15–18 October 2007
Glasgow, UK
http://www.bcpc.org/iapps2007/

9th Conference of the International Society for Plant Anaerobiosis
19–23 November 2007
Sendai, Japan
http://ispa-japan.miyakyo-u.ac.jp/

ASCB 47th Annual Meeting
1–5 December 2007
Washington, DC, USA
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