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Article Addendum

The Role of VIN3-LIKE Genes in Environmentally Induced Epigenetic Regulation of Flowering

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Addendum to:

A PHD Finger Protein Involved in Both the Vernalization and Photoperiod Pathways in Arabidopsis

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ABSTRACT

Given their sessile nature, it is critical for the survival of plants to adapt to their environment. Accordingly, plants have evolved the ability to sense seasonal changes to govern developmental fates such as the floral transition. Temperature and day length are among the seasonal cues that plants sense. We recently reported that *VIN3-LIKE 1* (*VIL1*) is involved in mediating the flowering response to both cold and day length via regulation of two related genes, *FLOWERING LOCUS C* (*FLC*) and *FLOWERING LOCUS M* (*FLM*), respectively.

Vernalization renders plants competent to flower after exposure to the prolonged cold of winter.[1,2] *Arabidopsis* exhibits facultative responses to both vernalization and photoperiod to initiate the floral transition. The facultative nature of the responses makes *Arabidopsis* a tractable genetic system to study these aspects of flowering time control.

In *Arabidopsis*, vernalization creates competence to flower via silencing of the potent floral repressor, *FLC*, in a mitotically stable manner.[3,4] Thus, the vernalization response is an environmentally induced epigenetic switch in that exposure to cold permanently affects the plants' developmental program. This epigenetic switch is associated with increased levels of *FLC* chromatin methylation on Histone H3 Lys 9 and Lys 27.[5,6] *VERNALIZATION INSENSITIVE 3* (*VIN3*) plays an essential role in this switch since no modifications to *FLC* chromatin occur in *vin3* mutants.[5] Furthermore, the levels of expression of *VIN3* mRNA are tightly correlated with the degree of the vernalization response.[5] *VIN3* encodes Plant HomeoDomain (PHD) finger-containing protein. PHD finger-containing proteins are often associated with protein complexes that are involved in chromatin remodeling.[7]

We performed a yeast two-hybrid screen to identify potential protein partners of VIN3. *VIN3-LIKE 1* (*VIL1*) was identified by this screen.[8] *VIL1* encodes a PHD finger-containing protein that is related to *VIN3*. As expected for proteins that are associated with VIN3, plants containing loss-of-function alleles of *VIL1* do not respond to vernalization. Furthermore, no vernalization-mediated histone modifications occur at *FLC* in *vil1* mutants similar to the situation in *vin3* mutants. Thus, by yeast two hybrid and genetic analysis, VIL1 is a bona fide VIN3 partner that is required for vernalization-mediated histone modifications at *FLC* chromatin. Unlike *VIN3*, the expression of *VIL1* does not change over the course of cold exposure. Rather, *VIL1* mRNA levels are affected by photoperiod. *VIL1* expression is significantly increased in non-inductive photoperiods (short days; SD). Consistent with this expression pattern, *vil1* mutants in the Columbia accession exhibit a SD-specific late-flowering phenotype. Furthermore, *VIL1* is required for attenuating expression of *FLOWERING LOCUS M*, a *FLC*-related gene, in a SD-specific manner. It is possible that the attenuation of *FLM* by *VIL1* has a role in creating the facultative nature of photoperiod response in *Arabidopsis* since *vil1* mutants tend towards an obligate photoperiod response (i.e., *vil1* mutants often fail to flower in SD).

In *Arabidopsis*, there are four *VIN3*-related genes, which we named as *VIL1 ~ VIL4*,[8] and which have also been called *VRN5* and *VEL1 ~ VEL3*.[9] The C-terminal domain is highly conserved among these genes and was named the VIN3-Interacting Domain (VID) since it is required for protein-protein interaction between VIN3 and VIL1. The effect of cold on the expression patterns of *VIN3*-related genes varies. For example, VIL2 and VIL3 are induced specifically by vernalizing cold exposures whereas others such as VIL1 are, for the most part, constitutively expressed. It will be interesting to determine the functions of the remaining *VIL* genes.

FLC is the main target for vernalization in *Arabidopsis*. Interestingly, *FLC* orthologs have not been found in vernalization-responsive varieties of cereals. However, in wheat, VRN2 appears to have a role equivalent to that of *FLC* in *Arabidopsis*.[10] *VRN2* encodes

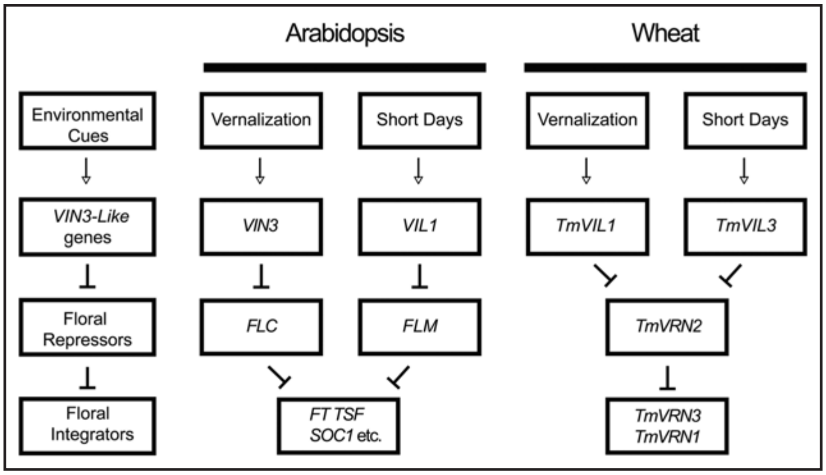

Figure 1. Proposed relationship of *VIN3* family genes to the regulatory network controlling flowering time in response to environmental cues in *Arabidopsis* and diploid wheat (adapted from ref. 16).

a ZCCT type zinc-finger protein that does not have a homolog in the *Arabidopsis* genome. In diploid wheat, down regulation of *VRN2* is correlated with the vernalization response.[11] Interestingly, wheat contains three *VIN3-LIKE* (*VIL*) genes, *TmVIL1*, *TmVIL2* and *TmVIL3*.[12] Furthermore, *TmVIL1* is up-regulated by vernalization.[12] However, whether *TmVIL1* has a direct role in the vernalization-mediated repression of *VRN2* in wheat has not yet been addressed. Similar to *VIL1*, *TmVIL3* shows elevated level of expression in SD. Furthermore, *VRN2* is downregulated in SD;[13,14] thus there is a correlation between the induction of *TmVIL* genes and the downregulation of the floral repressor *VRN2* similar to the *VIN3*/*FLC* and *VIL1*/*FLM* relationships (Fig. 1). Perhaps *VIN3*-related genes have similar roles both in *Arabidopsis* and in temperate wheat, but act on different target genes, possibly as a result of convergent evolution. Interestingly, the wheat gene *TmVRN3* is homologous to *FLOWERING LOCUS T* (*FT*) of *Arabidopsis*, and *TmVRN3* is repressed by *TmVRN2* as *FT* is repressed by *FLC*,[15] suggesting another similarity in the regulation of flowering time between *Arabidopsis* and temperate wheat (Fig. 1).

Although the PHD finger can be found in various eukaryotes, the VID is unique to plants. It is also noteworthy that *VIN3*-related genes can be found in various plant species, including rice, which does not have a vernalization response. It will be interesting to address whether the *VIN3*-related genes from various plant species are more broadly involved in relaying environmental signals to developmental programs.

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