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Article:

Song, Y. and Dixon, L.E. (Cover date: July 2026) If not cold, then short days. New Phytologist, 251 (1). pp. 8-10. ISSN: 0028-646X

<https://doi.org/10.1111/nph.71207>

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1 ***If not cold, then short-days***

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7 *Quote: “Reports of a different, non-low temperature dependent type of vernalization exist,*
8 *that of short-day vernalization (SDV)”*

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10 **Key words:** short-day vernalization, vernalization, Pooideae grasses, temperate climates,
11 crop adaption

Winter annual plants need low temperatures to overcome the block on reproductive development. This requirement is met via the process of vernalization (V) which has been widely used in annual cereal cultivation to enable over-winter growth and optimal spring flowering (Kim *et al.*, 2009). However, reports of a different, non-low temperature dependent type of vernalization exist, that of short-day vernalization (SDV). Here, SDs alone are able to overcome the reproductive block (Heide, 1984, Woods *et al.*, 2019, Schubert *et al.*, 2026). How the two types of vernalization arose, the relative importance and possible implications of both pathways has not been deeply considered, probably because the major winter annual crops, bread wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*), have traditionally been cultivated under environmental conditions which satisfy both the V and SDV requirements. That may now be changing with climate change and artificially via protocols which accelerate vernalization (Cha *et al.*, 2022). Unfortunately, our understanding of the SDV pathway has lagged behind that of V, however, a recently published article by Schubert *et al.* (2026) in *New Phytologist* changed this. A systematic and phylogenetic exploration on the prevalence of SDV across grass species from different Pooideae tribes provides compelling evidence that SDV is widespread. Furthermore, it found that SDV evolved early during the diversification of Pooideae, during the time this subfamily spread to temperate climates from tropical ones, requiring complex adaptive responses.

By conducting comparative transcriptomics for six Pooideae species, five SDV and one SD-responsive, Schubert *et al.* (2026) identify gene clusters linked to SDV and so propose a conserved molecular network across the Pooideae. This approach demonstrates the merit and potential of using cross species comparisons, only now possible through the advances in pan-genomics (Figure 1). This cross-species approach has the potential to rewrite our understanding of plant adaptation as already Schubert *et al.* identify conserved molecular signatures. This echoes recent findings regarding the multiple origins of spring *VRN1* alleles across the *Hordeum* genus, highlighting the convergent recruitment of an adaptive solution (Mascher *et al.*, 2025).

Interestingly, the central SDV responsive gene cluster contains well-known grass floral-development genes; *VERNALIZATION 2* (*VRN2*), *FLOWERING LOCUS T-LIKE 9* (*FTL9*), *FRUITFULL2* (*FUL2*) and *GENERAL REGULATORY FACTOR 14h* (*GF14h*). The identification of these genes immediately suggests common points of regulation between SDV and V. This is of huge interest for cereal crop development as characterizing if and how SDV intersects with V will not only contribute to understanding crop adaption and evolution, but

will also aid the development of elite crop varieties to confer flowering competency with minimum reliance on low temperature.

To this end, the functional characterization of *GF14h* via CRISPR mutants enables Schubert et al. (2026) to propose a SDV aware flowering model for the Pooideae grasses. This highlights the role of *GF14h* in regulating SDV where it promotes the expression of *VRN2* and *FTL4* under LDs before SDV, to repress reproductive development. Then following SDV, repression is released, and the floral promotion signal is integrated through the formation of FT1 florigen activation complex (FT1-FAC), which is also the central complex involved in V responsiveness. Notable overlap with the well-established regulatory pathway of V in crops is clear. During V, *VRN1* is expressed under low temperatures and represses *VRN2*, enabling the expression of active *FT1*. *VRN2* is also repressed by SDs and by LD after the chilling vernalization (Dubcovsky et al., 2006). Furthermore, the role of *VRN1* as downstream regulator of FAC and the regulatory role of *PPD1* promoted by LDs after vernalization has been included in the SD vernalization model. Recently *FT3*, a homolog of *FT1* (component of FAC complex), has been reported to function as a temperature-sensitive short-day florigen in bread wheat (Gauley et al., 2025) and so may also fit to this pathway. Understanding the molecular intersections of V and SDV is of great importance for providing the potential of adapting plants from V at higher latitudes to SDV at lower latitudes and for balancing the relative importance of each of these pathways within crops species for optimal local adaptation.

Phytohormones, such as auxin, gibberellin and cytokinin, play crucial roles in regulating plant growth and development by acting as endogenous signalling molecules and coordinating with exogenous factors (Mishra et al., 2022). For example, auxin is known for its role in regulating inflorescence, lateral root initiation, vascular tissue differentiation and leaf expansion, and it has also been found to affect flowering time, floret number and whole spike development (Wang et al., 2001, Mishra et al., 2022, Salisbury, 1955). The regulation of auxin on plant growth and development is mainly caused by its differential distribution and, interestingly, the second gene cluster identified by Schubert et al. (2026) contained a homolog of the auxin transport gene, *ABCB9*-like, which is downregulated under SDV conditions. Besides, other studies have also found that exogenous auxin application repressed flowering in SD plants (Cooke, 1954). This suggests a possible role of auxin involved in plants' reproductive development response to photoperiod during SDV. Another gene identified by Schubert et al. (2026) in the second cluster is the cytokinin signalling gene, *PHP3*. Similar to auxin, cytokinin level and distribution is also affected by the photoperiod (Macháčková et al., 1993). This

discovery, for the first time, reveals a broader view that links auxin transportation and cytokinin signalling to the molecular network of SDV, suggesting that these phytohormones potentially coordinate floral initiation with the photoperiodic signalling during SDV. This may be one of the physiologically ancient and conserved strategies used to achieve flowering competency after the expansion of Pooideae species from lower to higher latitude regions, where the photoperiod cue of V is distinct from SDV. This adaptive strategy provides a direction for developing SDV-responsive crop varieties by manipulating hormone-related genes.

Given the vulnerability of major cereal crops to unreliable and unpredictable autumn and winter temperatures, the findings of Schubert et al. (2026) provide a needed and welcome new breeding target. Through identifying and selecting SDV alleles in winter cereals flowering time and yield may be stabilized under warming climates, increasing the resilience of cereal crops. The SDV genes are conserved across diverse Pooideae species but in some species may have been recruited to multiple pathways. The characterisation presented strongly suggests that the major winter cereal crops wheat and barley contain relevant SDV genes. A detailed characterisation is now needed to identify which alleles need to be selected for requiring functional validation and an understanding of how manipulating the balance of SDV to V may impact final yield potential. Interestingly, recent work has identified that in barley and bread wheat, *VRN2* has roles beyond the V pathway, with respect to tiller outgrowth in barley (Montardit-Tarda *et al.*, 2025) and secondary tiller emergence rate and coleoptile tillers in bread wheat (Hirsz *et al.*, 2026). Continued functional understanding of V genes will provide a comprehensive framework that integrates SDV and V with plants' growth and development beyond flowering regulation.

The phenotypic characterisation, transcriptomics approach and computational analysis used by Schubert et al. (2026) provides a framework for how to study a wider range of species, identifying more phenotypic-specific molecular networks and charactering adaptive trait evolution. However, it must be acknowledged that the collection, cultivation and development of genomic resources for such diverse grasses is certainly not trivial.

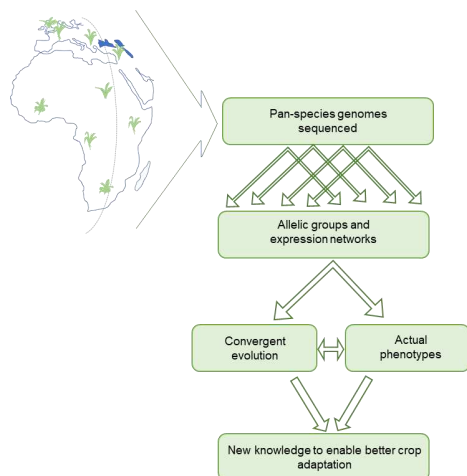


Figure 1: The power of using phylogenetically and climatically diverse cross-species comparisons to reveal novel genetic pathways underlying agriculturally important traits. This pipeline was used by Schubert et al to identify genetic candidates for SDV.

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