

Variation in gene regulation underlying annual and perennial flowering in Arabideae species

Jannice Friedman 

Department of Biology, Syracuse University, Syracuse, NY, USA

Correspondence

Jannice Friedman, Department of Biology, Syracuse University, Syracuse, NY, USA.
Email: friedman@syr.edu

Abstract

The diversity of life history strategies within the angiosperms illustrates the evolutionary flexibility of reproductive characteristics. The number of times an individual reproduces is a key life history trait, and transitions from iteroparous perennials to semelparous annuals have occurred frequently in the flowering plants. Despite the frequency of this evolutionary transition, and the importance of annuality versus perenniality to both agriculture and ecology, understanding the molecular and genetic mechanisms involved in perennial flowering is in their infancy. In this issue of *Molecular Ecology*, Kiefer et al. (2017) make significant progress towards understanding divergence in seasonal flowering between annual and perennial species in the Arabideae tribe of Brassicaceae. By combining a comparative approach with gene expression and sequence comparisons, they show that transcriptional differences in *FLC* orthologs, a floral inhibitor in *Arabidopsis thaliana*, have occurred repeatedly and underlie differences in flowering between annuals and perennials.

KEYWORDS

annual, *FLC*, flowering time, perennial, vernalization

A key parameter distinguishing annuals and perennials is the switch from vegetative growth to flowering. In annuals, this transition occurs once and is followed by senescence and death of the plant, while perennial plants cycle repeatedly through vegetative and reproductive modes. In temperate climates, these cycles are synchronized by the changing seasons, so that flowering is usually restricted to one time of year. When to initiate flowering is a critical life history trait that has been shaped over evolutionary time to maximize reproductive success in a particular environment. Plants use both environmental and endogenous cues to determine when to flower. Examples of environmental cues include changes in temperature and/or day length that reflect seasonal shifts. Endogenous cues include the transition from juvenile to adult phases, enabling competence to flower. Because perennial plants maintain vegetative growth after flowering, the perennial strategy requires differential behaviour of meristems on a single plant so that some remain in the vegetative state, while others undergo the floral transition (Battey & Tooke, 2002). Vegetative growth may be

maintained either by conserving some meristems in the vegetative state after flower initiation or by reverting back to vegetative development after flowering.

The genetic control of flowering is exceptionally well characterized in the annual plant *Arabidopsis thaliana*, and this knowledge is facilitating comparative studies seeking to understand flowering and life history strategies in related perennial plants (Albani & Coupland, 2010; Andrés & Coupland, 2012). An important insight for the mechanism underlying perennial cycling of vegetative and flowering stages came from studies of *Arabis alpina* where the *PEP1* ortholog of *FLC* was shown to be temporarily repressed by winter cold and then reactivated in spring (Wang et al., 2009), whereas in annual *A. thaliana*, it is stably repressed by cold. In their new paper, Kiefer et al. (2017) make significant progress by extending studies of *FLC* orthologs to more annual and perennial relatives. The authors first employ a phylogenetic approach to map annual/perennial transitions on 16 taxa in the Arabideae tribe, and then compare expression and sequence variation of *FLC* orthologs amongst a subset of annual and

perennial sister species. They show that annuals and perennials that differ in the cycling of vegetative growth and flowering, also differ in the cycling of transcription of the floral inhibitors of *FLC* orthologs (Figure 1). Next, they use an interspecific cross between an annual and perennial species to show that *cis*-regulatory changes at *FLC* contribute to transcriptional modifications underlying seasonal flowering differences. The combination of approaches gives them significant leverage to explore the genetic architecture of perenniality.

Previous work has shown that *FLC* orthologs in perennial species exhibit more complex gene structures compared to annual *A. thaliana* (Albani et al., 2012), suggesting a mechanistic link between complexity of the *FLC/PEP1* gene and life history. To explore the link between *FLC* and seasonal flowering, Kiefer et al. (2017) test six *Arabidopsis* species for their vernalization response and whether they harbor functional *FLC* alleles. Five of the six species showed obligate or facultative vernalization responses and are assumed to harbor active *FLC* alleles; however, they have similar gene structures implying that *FLC* duplication or complexity is not necessary for perennial life histories. However, when the authors assess whether differential expression of *FLC* orthologs is correlated

with life history, they find that in the perennial species the *FLC* orthologs are reactivated after vernalization, in contrast to the annual species which are stably repressed upon return to warm temperatures (Figure 1). This pattern is consistent with previously identified patterns for perennial *Arabidopsis alpina*, *Arabidopsis lyrata* and *Arabidopsis helleri*, suggesting a conserved mechanism for seasonal flowering.

To further explore the differential expression between annual and perennials, Kiefer and colleagues create a hybrid and backcross introgression lines between sister species, annual *Arabidopsis montbretiana* and perennial *A. alpina*. Each gene exhibits the expression pattern characteristic of the parent from which it originated, suggesting *cis*-acting sequence variation is conferring the observed differences in expression. They then identify genetic polymorphisms between *AmFLC* and *PEP1*, finding that clusters of SNPs in the 5' part of the first intron have the greatest evolutionary distance. This region coincides with previously identified regions of *FLC* that are required for stable repression of transcription after vernalization in annuals (Sheldon, Conn, Dennis, & Peacock, 2002), in particular the nucleation region and the region showing homology to the VRE and COLDAIR

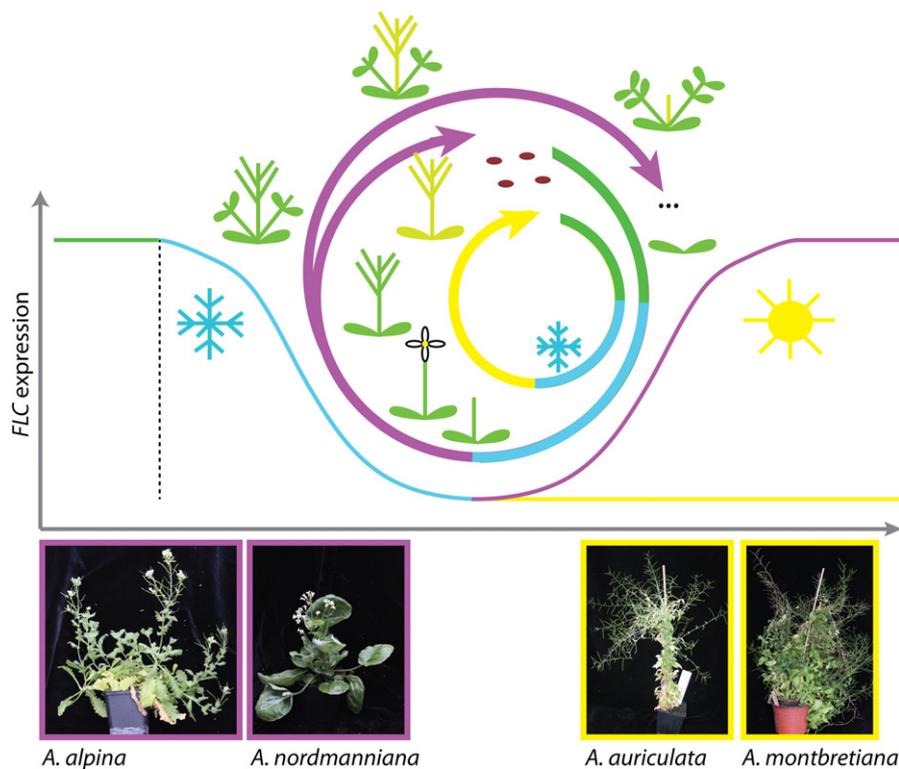


FIGURE 1 In the Brassicaceae, annuality evolved multiple times independently. Monocarpic annual plants complete their life cycle in one year (inner yellow circle), while polycarpic perennial plants undergo recurrent cycles of vegetative growth and reproduction (outer purple circle). Previously, *PEP1*, an ortholog of the floral repressor *FLC*, was identified as an important regulator of aspects of the perennial life cycle in *Arabidopsis alpina*. The *FLC* orthologs of both annuals and perennials are expressed before vernalization (green curve) and are repressed by vernalization (blue curve). However, after vernalization, the *FLC* orthologs are differentially expressed dependent on life history. In annuals such as *Arabidopsis auriculata* and *A. montbretiana*, *FLC* is stably repressed (yellow line). In perennials such as *A. alpina* and *Arabidopsis nordmanniana*, expression increases again after vernalization (purple line), thus inhibiting floral transition in some meristems and ensuring maintenance of vegetative growth for the next season. Expression studies in hybrid individuals of *A. alpina* and *A. montbretiana* led to the conclusion that the differential expression of their *FLC* orthologs is *cis*-mediated. Figure kindly provided by Christiane Kiefer

RNA encoding sequence of *FLC* (Heo & Sung, 2011; Sung et al., 2006). When Kiefer and colleagues broaden their analysis to genomic DNA sequences from more annual and perennial species, they find a similar distribution of SNP frequency peaks, that is, in the region homologous to the nucleation regions and upstream of the VRE. Due to the pattern of differentiation in comparisons either within or between life histories, they speculate that the region adjacent to the 5'-end of the VRE might diverge independently in annuals but be conserved in perennials, while the region at the 5'-end of intron 1 could be involved specifically in divergence between annuals and perennials.

These findings are intriguing because they suggest that similar genetic mechanisms might underlie repeated but independent evolutionary transitions. In this case, it appears that the annual life history might evolve independently by recurrent deactivation of a regulatory element required for perennial flowering. The inevitable question is whether this mechanism is generalizable to other annual–perennial transitions more distantly related to Brassicaceae. Because vernalization evolved independently in major lineages of the angiosperms (Amasino, 2005), it is unlikely that the same genes are implicated. However, it is intriguing to consider whether the same general molecular mechanisms are involved, that of stable repression of flowering inhibitors in annuals versus reactivation of inhibitors in perennials. A revolution in understanding perennial flowering might be found in a coordinated cycling of repressors of flowering with the periodicity of vegetative growth and flowering.

REFERENCES

- Albani, M. C., Castaings, L., Wötzel, S., Mateos, J. L., Wunder, J., Wang, R., ... Coupland, G. (2012). PEP1 of *Arabidopsis thaliana* is encoded by two overlapping genes that contribute to natural genetic variation in perennial flowering. *PLoS Genetics*, 8, e1003130.
- Albani, M. C., & Coupland, G. (2010). Chapter eleven – Comparative analysis of flowering in annual and perennial plants. *Current Topics in Developmental Biology*, 91, 323–348.
- Amasino, R. M. (2005). Vernalization and flowering time. *Current Opinion in Biotechnology*, 16, 154–158.
- Andrés, F., & Coupland, G. (2012). The genetic basis of flowering responses to seasonal cues. *Nature Reviews Genetics*, 13, 627–639.
- Batley, N. H., & Tooke, F. (2002). Molecular control and variation in the floral transition. *Current Opinion in Plant Biology*, 5, 62–68.
- Heo, J. B., & Sung, S. (2011). Vernalization-mediated epigenetic silencing by a long intronic noncoding RNA. *Science*, 331, 76–79.
- Kiefer, C., Severing, E., Karl, R., Bergonzi, S., Koch, M., Tresch, A., & Coupland, G. (2017). Divergence of annual and perennial species in the Brassicaceae and the contribution of cis-acting variation at *FLC* orthologues. *Molecular Ecology*, 26, 3437–3457.
- Sheldon, C. C., Conn, A. B., Dennis, E. S., & Peacock, W. J. (2002). Different regulatory regions are required for the vernalization-induced repression of *FLOWERING LOCUS C* and for the epigenetic maintenance of repression. *The Plant Cell*, 14, 2527–2537.
- Sung, S., He, Y., Eshoo, T. W., Tamada, Y., Johnson, L., Nakahigashi, K., ... Amasino, R. M. (2006). Epigenetic maintenance of the vernalized state in *Arabidopsis thaliana* requires LIKE HETEROCHROMATIN PROTEIN 1. *Nature Genetics*, 38, 706–710.
- Wang, R., Farrona, S., Vincent, C., Joecker, A., Schoof, H., Turck, F., ... Albani, M. C. (2009). PEP1 regulates perennial flowering in *Arabidopsis thaliana*. *Nature*, 459, 423–428.

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