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All's well that ends well: the timing of floral meristem termination

Author for correspondence:
Elena M. Kramer
Email: ekramer@oeb.harvard.edu

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Ya Min[1] and Elena M. Kramer[2]

[1]Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 012138, USA; [2]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA

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Summary

Floral meristem termination (FMT) represents one of the defining features of a floral meristem relative to a vegetative meristem. Timing of FMT is a major determinant of the total number of organs in a flower, and canalization toward relatively rapid FMT is considered to have been a major force in shaping angiosperm evolution. For decades, investigation of FMT has been focused on model systems that only produce four whorls of organs in a flower, while little is known about the molecular basis that underlies nature variation in the timing of FMT. Here, we hypothesize on how known pathways could have been modified to generate variation in FMT and explain how developing new model systems will help to deepen our understanding of the genetic control and evolution of FMT.

I. Introduction

All flowers start as a dome of undifferentiated cells – the floral meristem (FM; Steeves & Sussex, 1989). Despite a seemingly infinite variety of floral forms, the initial developmental pattern of the floral ground plan is strongly conserved (Smyth, 2018). The activities of the FM determine the position, timing of initiation, and number of all the floral organs, and variation in these parameters lay the foundation for floral morphological diversity. Over recent decades, we have gained an enormous amount of information on many aspects of the floral ground plan, but knowledge in one essential component is still surprisingly lacking: the genetic control and evolution of floral meristem termination (FMT), even though FMT represents one of the defining features of any FM. Here, we aim to address why understanding FMT is fundamental to our knowledge of floral development and evolution by elaborating on the following: how variation in FMT contributes to floral diversity and evolution; how this variation could be generated based on what we know about FMT in *Arabidopsis thaliana* (Arabidopsis)?; and, how new model systems are necessary to fill in the gaps in our understanding?

II. FMT and floral evolution and diversity

Every flower is a determinate structure, bearing a finite number of organs. When making a flower, FM produces floral organ primordia successively in spirals or whorls, and FMT is the coordinated termination of meristem activity following the production of a given number of organs (Fig. 1a, see also Min *et al.*, 2022a). The total number of organs in a flower is generally determined by two aspects of the FM: the FM width can influence the number of organs produced per whorl, or the number of

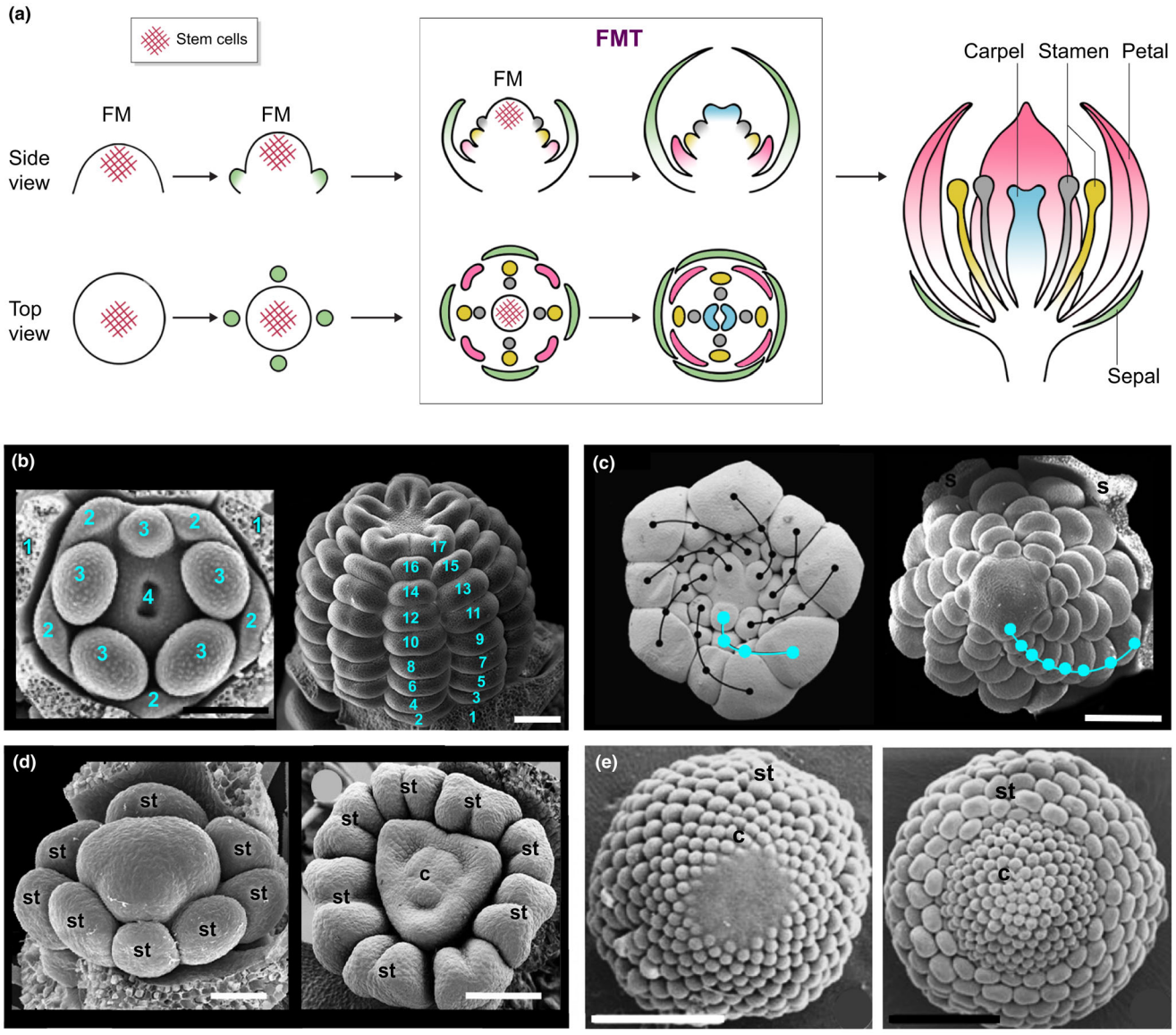

Fig. 1 Floral meristem termination (FMT) is one of the defining features of a floral meristem (FM) and variation in the timing of FMT is one of the foundations to floral morphological diversity. (a) Diagram of floral organ initiation and FMT during flower development: organs of the same whorl share the same colors (modified from Min *et al*., 2022b). (b) Different FMT timing can generate flowers with different whorls numbers using *Scrophularia nodosa* (left; modified from Endress, 2015) and *Aquilegia coerulea* (right, modified from Min & Kramer, 2020) as examples. Both flowers have floral organs initiated in whorls of five; number of whorls are indicated in blue. (c) Different FMT timing gives rise to different floral organ numbers in flowers with spiral phyllotaxy using *Austrobaileya scandens* (left; modified from Endress & Doyle, 2007) and *Nigella damascene* (right; modified from Zhao *et al*., 2011) as examples. Both flowers have the same numbers of parastichies (eight and five) but have different numbers of ranks, indicated as blue dots. (d) Before (left) and after (right) the initiation of the syncarpous gynoecium of *Cardiospermum gradiflorum*, during which the entire floral apex is consumed to build the carpel (modified from El Ottra *et al*., 2022). (e) Carpel initiation of *Anemone chinensis* with an apocarpous gynoecium. The floral apex is not immediately consumed as the FM persists to produce numerous individual carpels (modified from Ren *et al*., 2010). c, carpels; s, sepals; st, stamens. Bars: (b, c) 100 μm; (d) 50 μm; (e, left) 380 μm; (e, right) 0.5 mm.

parastichies produced in a flower with spiral phyllotaxy, while the timing of FMT determines the total number of whorls or ranks of parastichies (Fig. 1b,c). Although the number of organs per whorl can vary, it typically ranges only from three to six (Ronse De Craene, 2016). Similarly, the number of parastichies normally follows the Fibonacci series and rarely exceeds 21 (Endress & Doyle, 2007). Nonetheless, an incredible range of organ numbers (up to hundreds or even thousands) is observed in every major lineage of the flowering plants (Endress, 1990, 2011; Ronse De Craene, 2016), indicating that variation in the FMT is a critical contributor to variation in total floral organ numbers.

When considering evolutionary changes in the floral ground plan across angiosperms, several critical transitions are observed, including repeated shifts from variable to stable whorl numbers and a decrease in the total whorl numbers within a flower (Endress, 2011; Sauquet *et al*., 2017; Smyth, 2018), with both processes

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directly controlled by FMT. In other words, canalization toward relatively rapid FMT appears to have been a major force in shaping angiosperm evolution (Endress, 1990). Indeed, although significant ranges in total organ number are seen in all major lineages, in the largest clades, such as the asterids, rosids, and monocots, the extremes are set by a few outlier taxa with high whorl numbers (or novel innovations such as ring meristems, Kong & Becker, 2021), while the majority of the members have less than five whorls with little variation (Endress, 1990, 2011; Ronse De Craene, 2016, 2018). Meanwhile, other lineages (e.g. Nymphaeales, Magnoliales, and Ranunculales) exhibit large variation in organ numbers at all phylogenetic levels, even within the same individual, suggesting a high degree of flexibility in the timing of FMT. For instance, in a study of FMT variation in two sister species of *Aquilegia*, systematic counting of thousands of flowers revealed that while each species exhibited a normal distribution in whorl number, there were also distinct patterns of within-individual variation such that some plants had completely canalized whorl numbers but others varied (Min *et al.*, 2022a).

Interestingly, evolutionary variation in FMT most commonly gives rise to variation in stamen whorl number, while carpel numbers almost always remain fixed. When variation in carpel number does occur, it is strongly correlated with whether the flower forms a syncarpous or an apocarpous gynoecium (Endress, 2011; Ronse De Craene, 2018). Developmentally speaking, these two gynoecium types impose very different constraints on the nature of FMT. A syncarpous gynoecium consists of a whorl of carpels that are fused into a single functional unit that consumes the entire FM during initiation (Fig. 1d). Therefore, a tight alignment in the timing of FMT and carpel production is essential to ensure the success of seed and fruit production. By contrast, an apocarpous gynoecium is comprised of free carpels that each initiates and functions independently (Fig. 1e). Since the FM will not be immediately consumed as the first carpels arise, the coordination between primordia initiation and FMT can be more flexible. Perhaps not surprisingly, flowers with numerous carpels and/or a large variation in carpel numbers almost always have apocarpous gynoecia (Endress, 2011). This is particularly evident when lineages revert to apocarpy within otherwise syncarpous clades, such as many taxa in the Alismatales of the monocots, the Malvaceae of rosids, and the Apocynaceae of the asterids, all of which display a dramatic increase in carpel numbers than their syncarpous relatives (Igersheim *et al.*, 2001; Endress, 2011; Ronse De Craene, 2018).

III. How is FMT timed and how might timing vary?

The timing of FMT essentially determines the duration of stem cell proliferation in the FM. Over three decades, almost all of our knowledge of FM proliferation has been gained in the context of artificial selection (e.g. in agricultural crops; reviewed Li *et al.*, 2022) or mutagenesis approaches, both of which emphasize dramatic allelic effects that usually lead to a total cessation or massive overproliferation of stem cells (Chu *et al.*, 2019). Furthermore, our understanding regulation of FM proliferation is hindered by the fact that all currently established model systems and their close relatives invariably have only four whorls of floral organs, which provides no starting point for studies of natural variation in this trait. Currently, information about how FMT is precisely timed comes almost exclusively from Arabidopsis and has been reviewed in detail by Xu *et al.* (2019). Here, we will briefly summarize the known pathways and discuss how potential modifications on these pathways could give rise to different timing of FMT.

At the molecular level, FMT represents the termination of expression of the stem cell gene *WUSCHEL* (*WUS*) in the FM. Once a FM is formed, the expression of *WUS* can be detected in the stem cell niche in the center of the FM (Lenhard *et al.*, 2001; Lohmann *et al.*, 2001). *WUSCHEL* then directly activates the expression of *AGAMOUS* (*AG*), which controls stamen and carpel identities and is ultimately responsible for eliminating the expression of *WUS* (Lenhard *et al.*, 2001; Lohmann *et al.*, 2001). What is particularly interesting about this feedback loop is that these two interactions do not occur simultaneously: *AG* is activated before any floral organ primordia initiates, while the *WUS* repression takes place after the production of stamen primordia, with the window between these steps determining how long the stem cells can proliferate. Currently, two major pathways are known to directly fine-tune the timing of FMT in Arabidopsis: (1) AG activates a C2H2 zinc-finger transcription factor *KNUCKLES* (*KNU*), which directly represses *WUS* and (2) via a C2H2 zinc-finger transcriptional factor *SUPERMAN* (*SUP*) in *AG*-independent manner.

The mechanisms by which the AG-KNU-WUS pathway is used as a 'timer' for FMT have been demonstrated through a series of elegant experiments (Sun *et al.*, 2009, 2014, 2019; Shang *et al.*, 2021). *AGAMOUS* activates *KNU* by binding to the *KNU* promoter, which prevents the addition of epigenetic repressive markers onto *KNU*. It takes roughly two rounds of cell divisions to sufficiently dilute the repressive markers and allow the expression of *KNU*, during which the stamen primordia initiate and after which KNU immediately terminates *WUS*. To date, the functional conservation of *WUS*, *AG*, and the *WUS-AG* feedback loop has been widely demonstrated across angiosperms (Nardmann & Werr, 2006; Litt & Kramer, 2010), but the *AG-KNU-WUS* pathway has only been shown in Arabidopsis and tomato (Sun *et al.*, 2009, 2014; Bollier *et al.*, 2018), both systems that make flowers with only four whorls of organs. Since the duration of *KNU* activation only allows for the initiation of one whorl of stamens, it begs the question of how this pathway could function in taxa with more than two whorls of reproductive organs.

Nonetheless, it is reasonable to assume that, even if the function of *KNU* is lineage-specific, there is a functionally analogous factor or factors (hereafter refer to as 'X') in other taxa that are activated by *AG* and responsible for repressing *WUS*, because: the feedback loop between *AG* and *WUS* seems to be deeply conserved; and, there always appears to be a lag between *AG* expression and *WUS* termination (Kramer *et al.*, 2004; Jha *et al.*, 2020). Under this circumstance, two components of this pathway can theoretically be modified to produce more whorls (Fig. 2a): either the activation of *X* by *AG* can be delayed or the termination of *WUS* by *X* can be delayed. The former scenario would be possible if the *X* locus is covered by more epigenetic repressive markers, which would

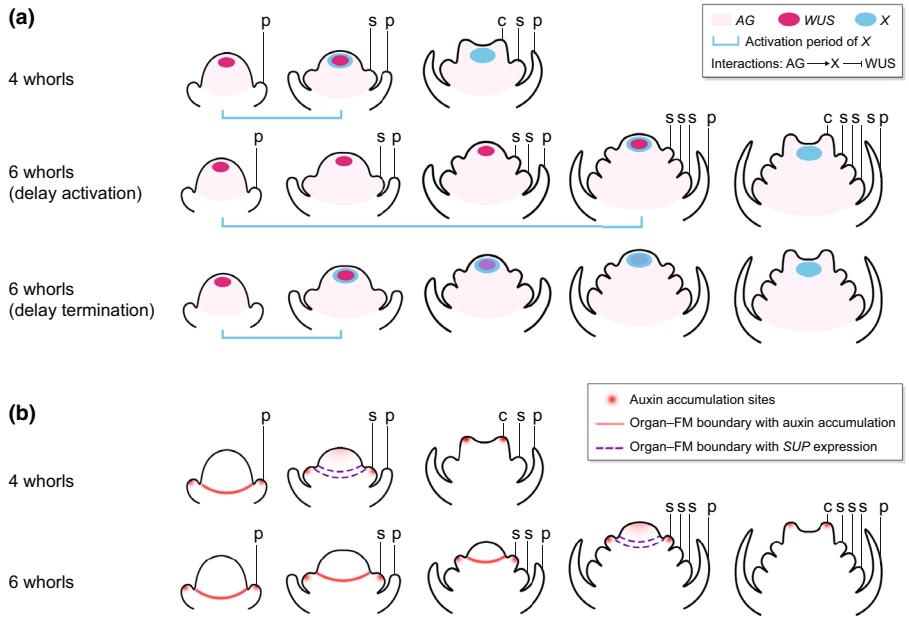

Fig. 2 How multiple whorls of organs can be theoretically generated based on our current understanding of the molecular basis of FMT. (a) Models of how modifications of the *AG-X-WUS* pathway could generate more than four whorls of organs (where X represents *KNU* or a functional analog). The four whorls diagram is based on what is known in Arabidopsis. Flowers with six whorls can be generated either by a delayed activation of *X* by *AG*, or by a delayed termination of *WUS* by *X*. (b) Model of how *SUP* could act as the signal for the initiation of the last whorl organ in a flower by changing auxin concentrations. When the newly initiated whorl is *not* the last whorl of stamens, relatively high auxin concentration (indicated in red) can be found at the organ-FM boundary and in the newly initiated primordia. If the newly initiated whorl is the last whorl of stamens, due to the expression of *SUP* at the organ-FM boundary (purple dotted lines), the auxin concentration at the organ boundary decreases while simultaneously increasing in the FM, which contributes to FMT. Under this scenario, increasing whorl number requires postponing *SUP* expression. Note, this diagram does not identify all potential locations of increased auxin concentration and the sepal whorls are not shown in any of the FM diagrams (i.e. a single whorl of sepals was assumed in all scenarios). c, carpels; p, petals; s, stamens.

require more rounds of cell division to sufficiently dilute, allowing time for more whorls of organ initiation. Alternatively, it may be that X has lower affinity for the *WUS* promoter, requiring more time for protein to accumulate and achieve *WUS* repression.

By contrast, the detailed mechanism by which *SUP* fine-tunes the timing of FMT is less clear. In Arabidopsis, *sup* mutants have an increase in stamen numbers at the expense of carpels (Bowman *et al.*, 1992). Mutants of *SUP* orthologs have been described in rice, *Petunia*, and *Medicago truncatula*, all of which exhibited somewhat similar phenotypes (Nakagawa *et al.*, 2004; Rodas *et al.*, 2021; Xu *et al.*, 2022), suggesting that *SUP* functions are likely to be generally conserved across lineages. Arabidopsis *sup* mutants have a higher total organ number than the wild-type (WT) because FMT is slightly delayed, and *SUP* promotes FMT by direct repression of auxin biosynthesis genes at the boundary (Xu *et al.*, 2018). This action appears to have a non-cell-autonomous effect on the FM such that in *sup* mutants, auxin levels are increased at the boundary but decreased in the center of the FM, which apparently leads to a slightly enlarged stem cell population and slightly prolonged activity of the FM (Xu *et al.*, 2018). This observation may be explained by a subsequent study that demonstrated that low levels of auxin signaling are crucial for maintaining the stem cell niche in the meristem (Ma *et al.*, 2019). Although evidence suggests that *SUP* regulates FMT in an *AG*-independent manner (Prunet *et al.*, 2017), the details of this mechanism remain unclear.

The very narrow expression domain of *SUP* in the Arabidopsis FM, both spatially and temporally, is intriguing because it is only expressed at the boundary between the stamen whorl and the carpel whorl immediately before the initiation of carpels, which are the last whorl of organs to be produced (Fig. 2b). Floral organ initiation is an iterative process: the initiation of a new whorl of organs also means the establishment of a new boundary between the new whorl and the remaining FM, and this iteration ends with the production of carpels. As discussed above, the subtle changes in auxin levels observed in *sup* mutants are suggestive that the inception of FMT requires a certain threshold level of auxin (Xu *et al.*, 2018). Taking all this information together, one plausible model (Fig. 2b) could be that during the early organ initiation process, auxin concentration remains low in the FM and slightly higher in the newly formed boundary. However, when the last whorl of stamen primordia is initiating, the expression of *SUP* leads to a decrease in auxin concentration at the boundary and a slight increase in concentration in the remaining FM itself, and this change disrupts the consistent iteration and acts as a signal that it is time to stop initiating organs. Thus, delaying expression of *SUP* could be critical to delay in FMT.

IV. How can we learn more?

Although it is not impossible to test the abovementioned models in Arabidopsis, a large amount of molecular engineering would be required, particularly because both *AG* and *WUS* are highly pleiotropic in their developmental functions. Alternatively,

systems with both natural variation in the timing of FMT and molecular genetic tools could be utilized, such as many taxa in the Ranunculales (Wang *et al.*, 2015; Damerval & Becker, 2017). For instance, *Aquilegia* species share the same number of whorls of all floral organs with the exception of the stamen whorls, which often vary (Munz, 1946; Tucker & Hodges, 2005). This natural variation in stamen whorl number provides an outstanding opportunity to investigate the regulation of FMT: a flower with earlier FMT will have fewer whorls of stamens than a flower that experiences later FMT. Moreover, recent development of a number of tools in *Aquilegia* has established a framework for the genetic study of FMT, and preliminary results have already shown a number of potential differences in FMT between Arabidopsis and *Aquilegia* (Min & Kramer, 2020; Min *et al.*, 2022b). Quantitative live-imaging of the *Aquilegia* FM revealed that, unlike Arabidopsis, the termination of stem cell proliferation and carpel initiation is not synchronized (Min *et al.*, 2022b), raising an intriguing question as to whether this reflects a difference between apocarpous (*Aquilegia*) and syncarpous (Arabidopsis) gynoecia and their relationships with FMT. QTL mapping of variation in whorl numbers in two sister species of *Aquilegia* unveiled complex genetic architecture and provided the first list of candidate genes potentially involved in the regulation of natural variation in the timing of FMT (Min *et al.*, 2022a). Hopefully, further studies of *Aquilegia* and other suitable model systems will help us to understand how conserved the known FMT pathways actually are and, most importantly, what kinds of molecular mechanisms underlie their critical variation.

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Competing interests

None declared.

ORCID

Elena M. Kramer https://orcid.org/0000-0002-5757-1088
Ya Min https://orcid.org/0000-0002-7526-4516

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