

Flowering Regulation in *Arabidopsis thaliana*

Subjects: Plant Sciences

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Definition

Flowering is one of the most critical developmental transitions in plants' life. The irreversible change from the vegetative to the reproductive stage is strictly controlled to ensure the progeny's success. In *Arabidopsis thaliana*, seven flowering genetic pathways have been described under specific growth conditions. However, the evidence suggests that these pathways are tightly interconnected in a complex multilevel regulatory network. Here we summarized the information of our recent publication.

1. Introduction

Flowering transition is a fundamental trait in plant development that marks the end of the vegetative phase and the beginning of the reproductive state. During this process, in *Arabidopsis thaliana* (hereafter *Arabidopsis*), a species from the Brassicaceae family, the Shoot Apical Meristem (SAM) becomes an Inflorescence Meristem (IM), which develops the Floral Meristems (FMs) at its flanks ^[1]. Then, the FMs differentiate into the flower organs ^[2].

The integration of developmental and physiological cues and the response to environmental signals forecast the best time for flowering to ensure success in reproduction and the offspring's viability ^[3].

In *Arabidopsis*, seven flowering genetic pathways have been proposed. These pathways respond to different signals such as: long-day (LD) photoperiod ^{[4][5][6]}; gibberellins (GA) ^{[7][8]}; vernalization ^[9], environmental autonomous cues ^{[10][11]}; thermal regulation ^{[12][13]}; aging ^{[14][15]} and trehalose 6-phosphate (T6P) ^[16]. Also, it has been considered that different pathways converge into a few transcription factors (TFs) known as integrators of flowering time: FLOWERING LOCUS C (FLC), FLOWERING LOCUS T (FT); SUPPRESSOR OF OVER EXPRESSION OF CONSTANS (SOC1) and, LEAFY (LFY) ^{[17][18][19][20]}. The latter is one of the first genes induced at the primordial cells committed to forming the FM ^[21], and it is essential for floral developmental progression.

This hierarchical scheme of flowering transition has changed over time and the current model proposes a complex genetic network of about 300 genes that underlies floral transition ^[22].

2. Regulation of Flowering Repressors

Premature reproduction under suboptimal environmental conditions or at the early stages of development has implications on pollination and seed formation, with repercussions on the species' fitness ^[23]. Therefore, flowering repressors are as relevant as promoter factors since they maintain the vegetative phase until specific signals trigger the reproductive transition. In *Arabidopsis*, these repressors were identified from early flowering loss of function mutants or late flowering overexpressor mutants ^{[11][24][25][26]}.

One of these flowering repressors is *FLC* ^[24], a MADS-box transcription factor (TF) expressed during the embryonic and vegetative phases of development ^[27]. FLC negatively regulates important flowering promoters such as SOC1 (another MADS-box gene) and FT ^[28].

When plants reach a developmental stage for flowering competence, *FLC* must be silenced. Multiple chromatin modifiers and RNA-binding proteins participate in *FLC* transcriptional and posttranscriptional regulation during this process ^{[10][29]}. Two possible mechanisms have been proposed. The first one considered a set of antisense long noncoding RNAs (lncRNAs) collectively called *COLD INDUCED LONG*

ANTISENSE INTRAGENIC RNAs (COOLAIR), which are transcribed from the 3'-end of *FLC* and proximately polyadenylated by FCA, FPA, and FY, and spliced by PRP8 [30]. Some of the *COOLAIR* variants could lead to FLOWERING LOCUS D (FLD) recruitment, which demethylates H3K4me₂, reducing the transcription of both sense and antisense *FLC* mRNAs [31]. Alternatively, there is evidence that FCA binds to CURLY LEAF (CLF), a Polycomb repressive complex (PRC2) subunit, in the presence of *COOLAIR* for H3K27me₃ deposition at the *FLC* locus [32].

Importantly, *FLC* is also subject to epigenetic repression during vernalization, which accelerates *Arabidopsis* flowering transition when plants return to optimal growth temperatures [33]. On the contrary, suboptimal growth temperatures (5–16 °C) negatively affect flowering in many natural accessions of *Arabidopsis* [34]. In this case, FLOWERING LOCUS M (*FLM*; a member of the *FLC* clade) is subject to temperature-dependent alternative splicing that results in the inclusion of either the second (*FLM*-β) or the third exon (*FLM*-δ) [35]. At lower temperatures, the *Arabidopsis* SPLICING FACTOR 1 (*AtSF1*) preferentially binds to the first intron branch site of *FLM* pre-mRNA producing the flowering-repressive *FLM*-β isoform. Accordingly, the *atsf1-2* mutant, which has very low levels of *FLM*-β and significantly higher levels of *FLM*-δ, is early flowering, but it has lost its sensitivity to temperature control [36]. It seems the net reduction in the abundance of *FLM*-β at optimal temperatures is sufficient to disrupt the formation of the repressive complex with SVP [35][37].

3. Endogenous Signals in Flowering Transition

Plant's endogenous cues that participate in flowering transition are present independently of the season, although environmental signals influence them. GAs hormones play an essential role in this process, as well as T6P, which constitutes a sensor of sugar availability and hence the plant's reserves to support reproduction [8][16]. Both signals are interconnected with the miR156 - SQUAMOSA BINDING PROTEIN LIKE (SPLs) - miR172 regulatory module [15] and the MADS-domain TFs to induce flowering transition.

As the plant ages, miR156 levels gradually decrease, allowing SPL mRNAs accumulation. In turn, SPL9, SPL10, and SPL15 induce reproductive transition by regulating genes related to flowering and binding to the *MIR172B* promoter [38][39]. Subsequently, the accumulation of miR172 indirectly promotes flowering transition by targeting *APETALA 2 (AP2)* and *AP2*-like flowering repressors, which repress *SPL3*, *SPL4*, and *SPL5 (SPL3/4/5)* genes [38][40].

GAs constitute a group of tetracyclic diterpene compounds that have multiple functions in plant development. It was Lang (1957) who first described the effect of these hormones as bloom inducers [41]. Specifically, high levels of GA₄ correlate with strong induction of *LFY* and *AP1* at the incipient FM [42].

Induction of *SPL3/4/5* by GA in the SAM is mediated by *SOC1* [8][43]. Furthermore, GAs are required to release *SPL15* from DELLAs, REPRESSOR OF *ga1-3* (RGA), and GIBBERELIC ACID INSENSITIVE (GAI) inhibition. *SPL15* then associates with *SOC1*, which, in collaboration with the REF6 and MED18 complex, induce *FUL* and *MIR172B* [39]. Additionally, GAs are important for upregulation of *SPL10*, which indirectly contributes to *FT* induction [44][38].

Interestingly, DELLA/GA signaling affects *SPL9* function by two opposing mechanisms. On one hand, GA-induced ubiquitination of RGA is required for *SPL9* to induce *SOC1* [45]. On the other hand, *SPL9* seems to require the presence of DELLAs to induce *AP1* transcription, since *SPL9*-mediated expression of *AP1* strongly decreases when plants are treated with GAs. The latter mechanism indicates that DELLAs also participate as co-activators [45].

Besides SPLs, GA signaling contributes to flowering transition by regulating the expression and activity of some MADS-box TFs in different manners (Figure 1). For example, *FLC* binding to *SOC1* and *FT* regulatory regions is enhanced in the presence of RGA; thereby, its degradation by the addition of GA₃ reduces *FLC* repressive action [46]. Moreover, GAs induce *SOC1* through the activity of NF-Y, or by downregulation of GATA NITRATE-INDUCED, CARBON METABOLISM INVOLVED (GNC), and its paralog GNC-

LIKE (GNL), which encode direct repressors of *SOC1* [47][48].

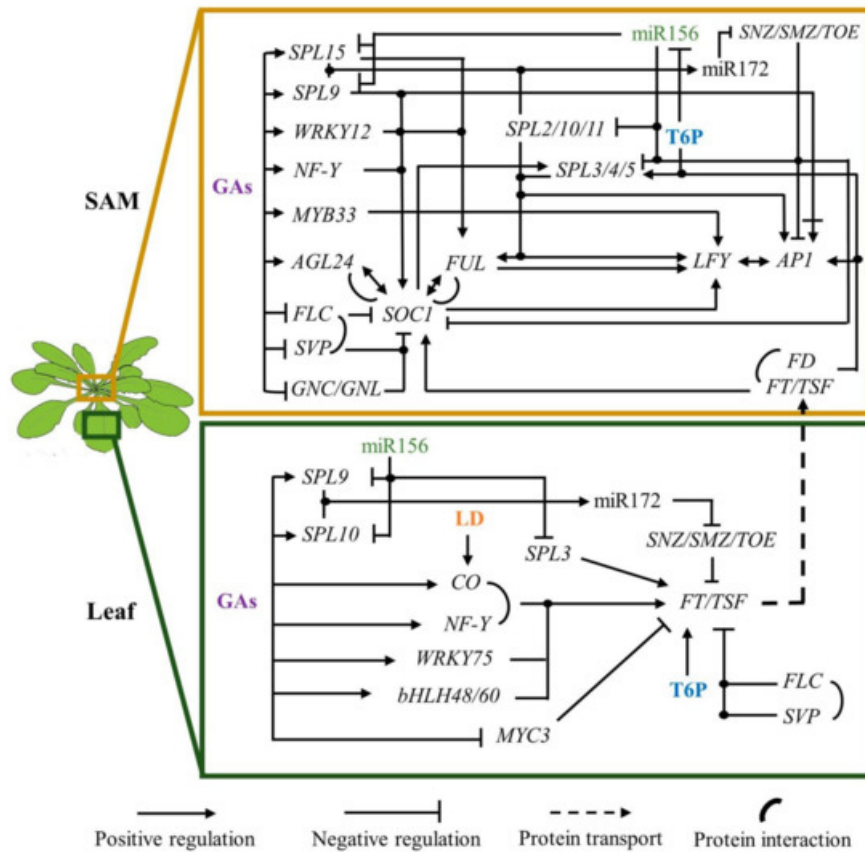


Figure 1. Gene regulatory network that promotes flowering transition in response to endogenous cues. Intricate regulations among the miR156-SPLs-miR172 module, and GAs and T6P signaling lead to *FT* induction in the leaves and *LFY* and *API* at the flanks of the IM. MADS-box, SPLs, AP2-like, and WRKY TFs have a preponderant role in flowering transition. SPL9 dual regulation on *API* (positive and negative bars), implies that in the presence of DELLAs, *API* is induced, but GA treatment drastically reduces it. Line intersections with dots indicate molecular interactions.

Also, DELLA proteins inactivate some of the WRKY TF family members implicated in flowering. WRKY75 and WRKY71 are direct regulators of *FT*, and WRKY71 also binds to *LFY*, although it is not clear if its TF activity depends on GA signaling [49][50]. Furthermore, WRKY12, in association with SPL10, induces *MIR172B*, while WRKY13 and SPL10 repress it [51]. Both of them interact with GAI and RGA-LIKE 1 (RGL1), and the degradation of these DELLAs by GAs enables WRKY12 to upregulate *FUL* expression directly and *SOC1* indirectly [52]. Subsequently, *FUL* induces flowering partly in collaboration with *SOC1* [53]. *SOC1* and *FUL* suppress *SVP* repression over *GA20OX2*. Thus, by lowering the repressor activity of *SVP*, GA levels rise, reinforcing flowering transition [54]. *SOC1* and *AGL24* mutual induction is also enhanced in response to GA [55]. Finally, XAANTAL2 (*XAL2*) is another member of the MADS-box family involved in flowering, probably in response to GA and independently of *SOC1*, since the double mutant *xal2-2 soc1-7* was unable to flower in response to GA_3 treatment after 88 days under SD conditions [56].

GAs regulation of MADS-box genes leads to the induction of *LFY* expression [57]. However, GAs can upregulate *LFY* expression by an independent mechanism. MYB33 accumulates in the shoot apex in response to GA_4 addition [58]. Furthermore, MYB33 binds to a highly conserved region in the *LFY* promoter [59].

The carbohydrates were long considered to be involved in the vegetative to reproductive transition [60]. However, the mechanisms by which sugars regulate flowering are not yet completely understood. Nevertheless, T6P signaling is critical for flowering transition regardless of day length [16]. T6P is produced from glucose-6-phosphate and uridine diphosphate (UDP)-glucose by the TREHALOSE-6-PHOSPHATE

SYNTHASE 1 (TPS1) [61]. T6P cascade induces *FT* and its closest homolog *TSF* in a CO-independent manner [16]. Additionally, *TPS1* is highly expressed in the IM, and its overexpression reverts the late-flowering phenotype of *ft-10*, suggesting that T6P acts independently or downstream of FT regulation [16].

Under SD photoperiod, T6P positively regulates the expression of *SPL3/4/5* at the SAM in a partially independent manner of miR156 decreasing by aging [16]. However, there is also evidence that an increase in endogenous sugar levels represses miR156 [62][63].

The close relationship between SPL and MADS-box TFs, as well as their response to endogenous and environmental cues during plant's phase transitions, strongly suggest that they are part of the same gene regulatory network (Figure 1). Moreover, it has been suggested that both groups of proteins act as pioneer transcription factors, binding, and opening inaccessible chromatin by recruiting chromatin remodeling complexes [64].

4. Long-Day Photoperiod and High-Temperature Function as Inductive Signals

Day length and high permissible temperatures are important signals to induce flowering in *A. thaliana*. Detection of photoperiod relies primarily on CO protein, a B-box-type zinc finger TF with a CCT domain, that accumulates during the day in the vascular tissue [4]. CONSTITUTIVE PHOTOMORFOGENIC 1 (COP1) and SUPPRESSOR OF PHYA-105S 1 (COP1/SPA1) complex ubiquitinates CO protein to be degraded by the proteasome at night. During the diurnal phase of long-day (LD)-photoperiod, cryptochromes 1 and 2, and phytochrome A are activated by blue and far-red light, respectively, inhibiting COP1/SPA1 activity. This action allows CO accumulation in the afternoon [65][66].

CO induces *FT* expression [18] which is translated and systemically travels from rosette leaves to the SAM to induce flowering [67][68]. Once they reach the SAM, FT interacts with the bZIP transcription factor FD via the 14-3-3 growth response factors [69]. Moreover, the FT-FD complex regulates the expression of *SPL3/4/5* in the IM, and they directly or in association with FD upregulate *FUL*, *LFY*, and *AP1* [70][71].

PHYTOCHROME INTERACTING FACTOR 4 (PIF 4) and its orthologs PIF5 and PIF7 are responsible for inducing *FT* and *TSF* expression in response to high temperature under short-day conditions [72][73]. Interestingly, at 27 °C, the H2A.Z-nucleosomes levels decreased at the *FT* locus, relaxing the chromatin and favoring the union of PIF4 to *FT* DNA [72]. It seems, therefore, that LD-photoperiod and high temperature are signals that can be separated, however, more research is required to establish their possible synergism.

The actual hierarchical flowering model proposed that different inputs converge into the integrators that transduce these signals to the FM identity genes [1]. Alternatively, we propose that endogenous signals can transversally dictate whether the plants remain in the vegetative phase or initiate the reproductive state. In this view, miR156, the DELLA proteins, and possibly low concentration of certain carbohydrates maintain the vegetative state, while miR172, GA, and T6P allow the reproductive phase change. Inductive signals like LD-photoperiod and temperature accelerate the flowering transition process in plants such as *Arabidopsis*, in part, by upregulating *FT* in the leaves and a group of the SPLs and MADS-box genes in the apical meristem. This ensures that flowering happens when the external conditions are optimal for those species.

References

1. Miguel A. Blázquez; Cristina Ferrándiz; Francisco Madueño; François Parcy; How Floral Meristems are Built. *Plant Molecular Biology* **2006**, 60, 855-870, 10.1007/s11103-006-0013-z.
2. Enrico S. Coen; Elliot M. Meyerowitz; The war of the whorls: genetic interactions controlling flower development. *Nature* **1991**, 353, 31-37, 10.1038/353031a0.
3. Israel Ausin; Carlos Alonso-Blanco; Jose-Miguel Martinez-Zapater; Environmental regulation of flowering. *The*

International Journal of Developmental Biology **2004**, *49*, 689-705, 10.1387/ijdb.052022ia.

4. Joanna Putterill; Frances Robson; Karen Lee; Rüdiger Simon; George Coupland; The CONSTANS gene of Arabidopsis promotes flowering and encodes a protein showing similarities to zinc finger transcription factors. *Cell* **1995**, *80*, 847-857, 10.1016/0092-8674(95)90288-0.
5. Paula Suárez-López; Kay Wheatley; Frances Robson; Hitoshi Onouchi; Federico Valverde; George Coupland; CONSTANS mediates between the circadian clock and the control of flowering in Arabidopsis. *Nature* **2001**, *410*, 1116-1120, 10.1038/35074138.
6. Takato Imaizumi; Steve A. Kay; Photoperiodic control of flowering: not only by coincidence. *Trends in Plant Science* **2006**, *11*, 550-558, 10.1016/j.tplants.2006.09.004.
7. Miguel A. Blazquez; Roland Green; Ove Nilsson; Michael R. Sussman; Detlef Weigel; Gibberellins Promote Flowering of Arabidopsis by Activating the LEAFY Promoter. *The Plant Cell* **1998**, *10*, 791, 10.2307/3870665.
8. Aimone Porri; Stefano Torti; Maida Romera-Branchat; George Coupland; Spatially distinct regulatory roles for gibberellins in the promotion of flowering of Arabidopsis under long photoperiods. *Development* **2012**, *139*, 2198-2209, 10.1242/dev.077164.
9. Candice C. Sheldon; Dean T. Rouse; E. Jean Finnegan; W. James Peacock; Elizabeth S. Dennis; The molecular basis of vernalization: The central role of FLOWERING LOCUS C (FLC). *Proceedings of the National Academy of Sciences* **2000**, *97*, 3753-3758, 10.1073/pnas.060023597.
10. Gordon G Simpson; The autonomous pathway: epigenetic and post-transcriptional gene regulation in the control of Arabidopsis flowering time. *Current Opinion in Plant Biology* **2004**, *7*, 570-574, 10.1016/j.pbi.2004.07.002.
11. M Koornneef; C Alonso-Blanco; H Blankestijn-De Vries; C J Hanhart; A J Peeters; Genetic interactions among late-flowering mutants of Arabidopsis. *Genetics* **1998**, *148*, 885-892.
12. Miguel Blazquez; Ji Hoon Ahn; Detlef Weigel; A thermosensory pathway controlling flowering time in Arabidopsis thaliana. *Nature Genetics* **2003**, *33*, 168-171, 10.1038/ng1085.
13. Jeong Hwan Lee; Seong Jeon Yoo; Soo Hyun Park; Ildoo Hwang; Ji Hoon Ahn; Role of SVP in the control of flowering time by ambient temperature in Arabidopsis. *Genes & Development* **2007**, *21*, 397-402, 10.1101/gad.1518407.
14. Gang Wu; R. Scott Poethig; Temporal regulation of shoot development in Arabidopsis thaliana by miR156 and its target SPL3. *Development* **2006**, *133*, 3539-3547, 10.1242/dev.02521.
15. Youbong Hyun; René Richter; George Coupland; Competence to Flower: Age-Controlled Sensitivity to Environmental Cues. *Plant Physiology* **2017**, *173*, 36-46, 10.1104/pp.16.01523.
16. Vanessa Wahl; Jathish Ponnu; Armin Schlereth; Stéphanie Arrivault; Tobias Langenecker; Annika Franke; Regina Feil; John E. Lunn; Mark Stitt; Markus Schmid; et al. Regulation of Flowering by Trehalose-6-Phosphate Signaling in Arabidopsis thaliana. *Science* **2013**, *339*, 704-707, 10.1126/science.1230406.
17. Horim Lee; Sung-Suk Suh; Eunsook Park; Euna Cho; Ji Hoon Ahn; Sang-Gu Kim; Jong Seob Lee; Young Myung Kwon; Ilha Lee; The AGAMOUS-LIKE 20 MADS domain protein integrates floral inductive pathways in Arabidopsis. *Genes & Development* **2000**, *14*, 2366-2376, 10.1101/gad.813600.
18. Alon Samach; Hitoshi Onouchi; Scott E. Gold; Gary S. Ditta; Zsuzsanna Schwarz-Sommer; Martin F. Yanofsky; George Coupland; Distinct Roles of CONSTANS Target Genes in Reproductive Development of Arabidopsis. *Science* **2000**, *288*, 1613-1616, 10.1126/science.288.5471.1613.
19. Jihyun Moon; Horim Lee; Minsoo Kim; Ilha Lee; Analysis of Flowering Pathway Integrators in Arabidopsis. *Plant and Cell Physiology* **2005**, *46*, 292-299, 10.1093/pcp/pci024.
20. Scott D. Michaels; Edward Himelblau; Sang Yeol Kim; Fritz M. Schomburg; Richard M. Amasino; Integration of Flowering Signals in Winter-Annual Arabidopsis. *Plant Physiology* **2005**, *137*, 149-156, 10.1104/pp.104.052811.
21. F.D. Hempel; D. Weigel; M.A. Mandel; G. Ditta; P.C. Zambryski; L.J. Feldman; M.F. Yanofsky; Floral determination and expression of floral regulatory genes in Arabidopsis. *Development* **1997**, *124*, 3845-3853, 10.1242/dev.124.19.3845.
22. Frédéric Bouché; Guillaume Lobet; Pierre Tocquin; Claire Périlleux; FLOR-ID: an interactive database of flowering-time gene networks in Arabidopsis thaliana. *Nucleic Acids Research* **2016**, *44*, D1167-D1171, 10.1093/nar/gkv1054.
23. Giorgio Perrella; Elisa Vellutini; Anna Zioutopoulou; Eirini Patitaki; Lauren R. Headland; Eirini Kaiserli; Let it bloom: cross-talk between light and flowering signaling in Arabidopsis. *Physiologia Plantarum* **2020**, *169*, 301-311, 10.1111/ppl.13073.
24. Candice C. Sheldon; Joanne E. Burn; Pascual P. Perez; Jim Metzger; Jennifer A. Edwards; W. James Peacock; Elizabeth S. Dennis; The FLF MADS Box Gene: A Repressor of Flowering in Arabidopsis Regulated by Vernalization and Methylation. *The Plant Cell* **1999**, *11*, 445, 10.2307/3870872.
25. Ulrike Hartmann; Susanne Hohmann; Klaus Nettessheim; Ellen Wisman; Heinz Saedler; Peter Huijser; Molecular cloning of SVP: a negative regulator of the floral transition in Arabidopsis. *The Plant Journal* **2000**, *21*, 351-360, 10.1046/j.1365-313x.2000.00682.x.
26. Katia C. Scortecci; Scott D. Michaels; Richard M. Amasino; Identification of a MADS-box gene, FLOWERING LOCUS M, that represses flowering. *The Plant Journal* **2001**, *26*, 229-236, 10.1046/j.1365-313x.2001.01024.x.
27. Weiwei Deng; Hua Ying; Chris A. Helliwell; Jen Taylor; W. James Peacock; Elizabeth S. Dennis; FLOWERING LOCUS C (FLC) regulates development pathways throughout the life cycle of Arabidopsis. *Proceedings of the National Academy*

- of Sciences **2011**, *108*, 6680-6685, 10.1073/pnas.1103175108.
28. Chris A. Helliwell; Craig C. Wood; Masumi Robertson; W. James Peacock; Elizabeth S. Dennis; The Arabidopsis FLC protein interacts directly in vivo with SOC1 and FT chromatin and is part of a high-molecular-weight protein complex. *The Plant Journal* **2006**, *46*, 183-192, 10.1111/j.1365-313x.2006.02686.x.
 29. Csaba Hornyik; Céline Duc; Katarzyna Rataj; Lionel C. Terzi; Gordon G. Simpson; Alternative polyadenylation of antisense RNAs and flowering time control. *Biochemical Society Transactions* **2010**, *38*, 1077-1081, 10.1042/bst0381077.
 30. Sebastian Marquardt; Oleg Raitskin; Zhe Wu; Fuquan Liu; Qianwen Sun; Caroline Dean; Functional Consequences of Splicing of the Antisense Transcript COOLAIR on FLC Transcription. *Molecular Cell* **2014**, *54*, 156-165, 10.1016/j.molcel.2014.03.026.
 31. Zhe Wu; Xiaofeng Fang; Danling Zhu; Caroline Dean; Autonomous Pathway: FLOWERING LOCUS C Repression through an Antisense-Mediated Chromatin-Silencing Mechanism. *Plant Physiology* **2020**, *182*, 27-37, 10.1104/pp.19.01009.
 32. Yongke Tian; Han Zheng; Fei Zhang; Shiliang Wang; Xiaoru Ji; Chao Xu; Yuehui He; Yong Ding; PRC2 recruitment and H3K27me3 deposition at FLC require FCA binding of COOLAIR. *Science Advances* **2019**, *5*, eaau7246, 10.1126/sciadv.aau7246.
 33. Scott Berry; Caroline Dean; Environmental perception and epigenetic memory: mechanistic insight through FLC. *The Plant Journal* **2015**, *83*, 133-148, 10.1111/tpj.12869.
 34. Ulrich Lutz; Thomas Nussbaumer; Manuel Spannagl; Julia Diener; Klaus Fx Mayer; Claus Schwechheimer; Natural haplotypes of FLM non-coding sequences fine-tune flowering time in ambient spring temperatures in Arabidopsis. *eLife* **2017**, *6*, e22114, 10.7554/elife.22114.
 35. David Posé; Leonie Verhage; Felix Ott; Levi Yant; Johannes Mathieu; Gerco C. Angenent; Richard Immink; Markus Schmid; Temperature-dependent regulation of flowering by antagonistic FLM variants. *Nature* **2013**, *503*, 414-417, 10.1038/nature12633.
 36. Keh Chien Lee; Kyung Sook Chung; Hee Tae Lee; Jae-Hyeok Park; Jeong Hwan Lee; Jeong-Kook Kim; Role of Arabidopsis Splicing factor SF1 in Temperature-Responsive Alternative Splicing of FLM pre-mRNA. *Frontiers in Plant Science* **2020**, *11*, 1-14, 10.3389/fpls.2020.596354.
 37. Giovanna Capovilla; Efthymia Symeonidi; Rui Wu; Markus Schmid; Contribution of major FLM isoforms to temperature-dependent flowering in Arabidopsis thaliana. *Journal of Experimental Botany* **2017**, *68*, 5117-5127, 10.1093/jxb/erx328.
 38. Gang Wu; Mee Yeon Park; Susan R. Conway; Jia-Wei Wang; Detlef Weigel; R. Scott Poethig; The Sequential Action of miR156 and miR172 Regulates Developmental Timing in Arabidopsis. *Cell* **2009**, *138*, 750-759, 10.1016/j.cell.2009.06.031.
 39. Youbong Hyun; René Richter; Coral Vincent; Rafael Martinez-Gallegos; Aimone Porri; George Coupland; Multi-layered Regulation of SPL15 and Cooperation with SOC1 Integrate Endogenous Flowering Pathways at the Arabidopsis Shoot Meristem. *Developmental Cell* **2016**, *37*, 254-266, 10.1016/j.devcel.2016.04.001.
 40. Jae-Hoon Jung; Pil Joon Seo; Seok Ki Kang; Chung-Mo Park; miR172 signals are incorporated into the miR156 signaling pathway at the SPL3/4/5 genes in Arabidopsis developmental transitions. *Plant Molecular Biology* **2011**, *76*, 35-45, 10.1007/s11103-011-9759-z.
 41. A. Lang; THE EFFECT OF GIBBERELLIN UPON FLOWER FORMATION. *Proceedings of the National Academy of Sciences* **1957**, *43*, 709-717, 10.1073/pnas.43.8.709.
 42. Sven Eriksson; Henrik Böhlenius; Thomas Moritz; Ove Nilsson; GA4 Is the Active Gibberellin in the Regulation of LEAFY Transcription and Arabidopsis Floral Initiation. *The Plant Cell* **2006**, *18*, 2172-2181, 10.1105/tpc.106.042317.
 43. Jae-Hoon Jung; Yun Ju; Pil Joon Seo; Jae-Hyung Lee; Chung-Mo Park; The SOC1-SPL module integrates photoperiod and gibberellic acid signals to control flowering time in Arabidopsis. *The Plant Journal* **2012**, *69*, 577-588, 10.1111/j.1365-313x.2011.04813.x.
 44. Johannes Mathieu; Levi Yant; Felix Mürdter; Frank Küttner; Markus Schmid; Repression of Flowering by the miR172 Target SMZ. *PLOS Biology* **2009**, *7*, e1000148, 10.1371/journal.pbio.1000148.
 45. Nobutoshi Yamaguchi; Cara M. Winter; Miin-Feng Wu; Yuri Kanno; Ayako Yamaguchi; Mitsunori Seo; Doris Wagner; Gibberellin Acts Positively Then Negatively to Control Onset of Flower Formation in Arabidopsis. *Science* **2014**, *344*, 638-641, 10.1126/science.1250498.
 46. Mingzhe Li; Fengying An; Wenyang Li; Mengdi Ma; Ying Feng; Xing Zhang; Hongwei Guo; DELLA proteins interact with FLC to repress flowering transition. *Journal of Integrative Plant Biology* **2016**, *58*, 642-655, 10.1111/jipb.12451.
 47. Xingliang Hou; Jiannan Zhou; Chang Liu; Lu Liu; Lisha Shen; Hao Yu; Nuclear factor Y-mediated H3K27me3 demethylation of the SOC1 locus orchestrates flowering responses of Arabidopsis. *Nature Communications* **2014**, *5*, 4601, 10.1038/ncomms5601.
 48. René Richter; Emmanouil Bastakis; Claus Schwechheimer; Cross-Repressive Interactions between SOC1 and the GATAs GNC and GNL/CGA1 in the Control of Greening, Cold Tolerance, and Flowering Time in Arabidopsis. *Plant Physiology* **2013**, *162*, 1992-2004, 10.1104/pp.113.219238.
 49. Yanchong Yu; Zhenhua Liu; Long Wang; Sang-Gyu Kim; Pil J. Seo; Meng Qiao; Nan Wang; Shuo Li; Xiaofeng Cao;

- Chung-Mo Park; et al. FengNing Xiang WRKY71 accelerates flowering via the direct activation of FLOWERING LOCUS T and LEAFY in Arabidopsis thaliana. *The Plant Journal* **2016**, *85*, 96-106, 10.1111/tpj.13092.
50. Liping Zhang; Ligang Chen; Diqiu Yu; Transcription Factor WRKY75 Interacts with DELLA Proteins to Affect Flowering. *Plant Physiology* **2018**, *176*, 790-803, 10.1104/pp.17.00657.
51. Zhenbing Ma; Wei Li; Houping Wang; Diqiu Yu; WRKY transcription factors WRKY12 and WRKY13 interact with SPL10 to modulate age-mediated flowering. *Journal of Integrative Plant Biology* **2020**, *62*, 1659-1673, 10.1111/jipb.12946.
52. Wei Li; Houping Wang; Diqiu Yu; Arabidopsis WRKY Transcription Factors WRKY12 and WRKY13 Oppositely Regulate Flowering under Short-Day Conditions. *Molecular Plant* **2016**, *9*, 1492-1503, 10.1016/j.molp.2016.08.003.
53. Vicente Balanzà; Irene Martínez-Fernández; Cristina Ferrándiz; Sequential action of FRUITFULL as a modulator of the activity of the floral regulators SVP and SOC1. *Journal of Experimental Botany* **2014**, *65*, 1193-1203, 10.1093/jxb/ert482.
54. Fernando Andrés; Aimone Porri; Stefano Torti; Julieta Mateos; Maida Romera-Branchat; José Luis García-Martínez; Fabio Fornara; Veronica Gregis; Martin M. Kater; George Coupland; et al. SHORT VEGETATIVE PHASE reduces gibberellin biosynthesis at the Arabidopsis shoot apex to regulate the floral transition. *Proceedings of the National Academy of Sciences* **2014**, *111*, E2760-E2769, 10.1073/pnas.1409567111.
55. Chang Liu; Hongyan Chen; Hong Ling Er; Hui Meng Soo; Prakash P. Kumar; Jin-Hua Han; Yih Cherng Liou; Hao Yu; Direct interaction of AGL24 and SOC1 integrates flowering signals in Arabidopsis. *Development* **2008**, *135*, 1481-1491, 10.1242/dev.020255.
56. Rigoberto V. Pérez-Ruiz; Berenice García-Ponce; Nayelli Marsch Martinez; Yamel Ugartechea-Chirino; Mitzi Villajuana-Bonequi; Stefan de Folter; Eugenio Azpeitia; José Dávila-Velderrain; David Cruz-Sánchez; Adriana Garay; et al. María De La Paz SanchezJuan M. Estévez-PalmasElena R. Álvarez-Buylla XAANTAL2 (AGL14) Is an Important Component of the Complex Gene Regulatory Network that Underlies Arabidopsis Shoot Apical Meristem Transitions. *Molecular Plant* **2015**, *8*, 796-813, 10.1016/j.molp.2015.01.017.
57. Jungeun Lee; Mijin Oh; Hanna Park; Ilha Lee; SOC1 translocated to the nucleus by interaction with AGL24 directly regulates LEAFY. *The Plant Journal* **2008**, *55*, 832-843, 10.1111/j.1365-313x.2008.03552.x.
58. Gregory F.W. Gocal; Candice C. Sheldon; Frank Gubler; Thomas Moritz; David J. Bagnall; Colleen P. Macmillan; Song F. Li; Roger W. Parish; Elizabeth S. Dennis; Detlef Weigel; et al. Rod W. King GAMYB-like Genes, Flowering, and Gibberellin Signaling in Arabidopsis. *Plant Physiology* **2001**, *127*, 1682-1693, 10.1104/pp.127.4.1682.
59. Miguel Blazquez; Detlef Weigel; Integration of floral inductive signals in Arabidopsis. *Nature* **2000**, *404*, 889-892, 10.1038/35009125.
60. Laurent Corbesier; Pierre Lejeune; Georges Bernier; The role of carbohydrates in the induction of flowering in Arabidopsis thaliana : comparison between the wild type and a starchless mutant. *Planta* **1998**, *206*, 131-137, 10.1007/s004250050383.
61. Matthew J. Paul; Lucia F. Primavesi; Deveraj Jhurrea; Yuhua Zhang; Trehalose Metabolism and Signaling. *Annual Review of Plant Biology* **2008**, *59*, 417-441, 10.1146/annurev.arplant.59.032607.092945.
62. Manuel Buendía-Monreal; C. Stewart Gillmor; Convergent repression of miR156 by sugar and the CDK8 module of Arabidopsis Mediator. *Developmental Biology* **2017**, *423*, 19-23, 10.1016/j.ydbio.2017.01.007.
63. Hang Zhao; Ke Lin; Lin Ma; Qingshuai Chen; Shuo Gan; Gang Li; Arabidopsis NUCLEAR FACTOR Y A8 inhibits the juvenile-to-adult transition by activating transcription of MIR156s. *Journal of Experimental Botany* **2020**, *71*, 4890-4902, 10.1093/jxb/eraa197.
64. René Richter; Atsuko Kinoshita; Coral Vincent; Rafael Martinez-Gallegos; He Gao; Annabel D. Van Driel; Youbong Hyun; Julieta L. Mateos; George Coupland; Floral regulators FLC and SOC1 directly regulate expression of the B3-type transcription factor TARGET OF FLC AND SVP 1 at the Arabidopsis shoot apex via antagonistic chromatin modifications. *PLOS Genetics* **2019**, *15*, e1008065, 10.1371/journal.pgen.1008065.
65. Zecheng Zuo; Hongtao Liu; Bin Liu; Xuanming Liu; Chentao Lin; Blue Light-Dependent Interaction of CRY2 with SPA1 Regulates COP1 activity and Floral Initiation in Arabidopsis. *Current Biology* **2011**, *21*, 841-847, 10.1016/j.cub.2011.03.048.
66. Li-Jun Liu; Yan-Chun Zhang; Qing-Hua Li; Yi Sang; Jian Mao; Hong-Li Lian; Long Wang; Hong-Quan Yang; COP1-Mediated Ubiquitination of CONSTANS Is Implicated in Cryptochrome Regulation of Flowering in Arabidopsis. *The Plant Cell* **2008**, *20*, 292-306, 10.1105/tpc.107.057281.
67. Laurent Corbesier; Coral Vincent; Seonghoe Jang; Fabio Fornara; Qingzhi Fan; Iain Searle; Antonis Giakountis; Sara Farrona; Lionel Gissot; Colin Turnbull; et al. George Coupland FT Protein Movement Contributes to Long-Distance Signaling in Floral Induction of Arabidopsis. *Science* **2007**, *316*, 1030-1033, 10.1126/science.1141752.
68. Katja E. Jaeger; Philip A. Wigge; FT Protein Acts as a Long-Range Signal in Arabidopsis. *Current Biology* **2007**, *17*, 1050-1054, 10.1016/j.cub.2007.05.008.
69. Silvio Collani; Manuela Neumann; Levi Yant; Markus Schmid; FT Modulates Genome-Wide DNA-Binding of the bZIP Transcription Factor FD. *Plant Physiology* **2019**, *180*, 367-380, 10.1104/pp.18.01505.
70. Ayako Yamaguchi; Miin-Feng Wu; Li Yang; Gang Wu; R. Scott Poethig; Doris Wagner; The MicroRNA-Regulated SBP-Box Transcription Factor SPL3 Is a Direct Upstream Activator of LEAFY, FRUITFULL, and APETALA1. *Developmental Cell*

2009, 17, 268-278, 10.1016/j.devcel.2009.06.007.

71. Jae-Hoon Jung; Hyo-Jun Lee; Jae Yong Ryu; Chung-Mo Park; SPL3/4/5 Integrate Developmental Aging and Photoperiodic Signals into the FT-FD Module in Arabidopsis Flowering. *Molecular Plant* **2016**, 9, 1647-1659, 10.1016/j.molp.2016.10.014.
72. S. Vinod Kumar; Doris Lucyshyn; Katja E. Jaeger; Enriqueta Alós; Elizabeth Alvey; Nicholas P. Harberd; Philip A. Wigge; Transcription factor PIF4 controls the thermosensory activation of flowering. *Nature* **2012**, 484, 242-245, 10.1038/nature10928.
73. Vinicius Costa Galvão; Anne-Sophie Fiorucci; Martine Trevisan; Jose Manuel Franco-Zorrilla; Anupama Goyal; Emanuel Schmid-Siegert; Roberto Solano; Christian Fankhauser; PIF transcription factors link a neighbor threat cue to accelerated reproduction in Arabidopsis. *Nature Communications* **2019**, 10, 1-10, 10.1038/s41467-019-11882-7.

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