New Phytologist

Review

Tansley insight

Biomolecular condensation programs floral transition to orchestrate flowering time and inflorescence architecture

Author for correspondence:
Cao Xu
Email:caoxu@genetics.ac.cn

Received: *12 June 2024*
Accepted: *11 September 2024*

Xiaozhen Huang[1,2], Yongfang Yang[1,2] and Cao Xu[1,2]

[1]Key Laboratory of Seed Innovation, Institute of Genetics and Developmental Biology, The Innovative Academy of Seed Design, Chinese Academy of Sciences, Beijing, 100101, China; [2]CAS-JIC Centre of Excellence for Plant and Microbial Science (CEPAMS), Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing, 100101, China

Contents

New Phytologist (2024)
doi: 10.1111/nph.20204

Key words: biomolecular condensation, floral transition, flowering time, inflorescence architecture, regulatory mechanism.

Summary

Biomolecular condensation involves the concentration of biomolecules (DNA, RNA, proteins) into compartments to form membraneless organelles or condensates with unique properties and functions. This ubiquitous phenomenon has garnered considerable attention in recent years owing to its multifaceted roles in developmental processes and responses to environmental cues in living systems. Recent studies have revealed that biomolecular condensation plays essential roles in regulating the transition of plants from vegetative to reproductive growth, a programmed process known as floral transition that determines flowering time and inflorescence architecture in flowering plants. In this Tansley insight, we review advances in how biomolecular condensation integrates developmental and environmental signals to program and reprogram the floral transition thus diversifies flowering time and inflorescence architecture.

I. Introduction

Biomolecular condensation

Biomolecular condensation is characterized by the formation of membraneless organelles or condensates that can exist in various physical states, including liquid, gel, and solid, depending on the specific conditions and components within cells. Through liquid–liquid phase separation (LLPS), biomolecules such as RNA, DNA, and proteins are sequestered into liquid-like condensates and reorganized in space and time, effectively compartmentalizing cellular biochemistry. The LLPS typically leads to the liquid state, while further maturation or aging can result in gel or solid states (Boeynaems *et al.*, 2018). LLPS is driven by multivalent interactions, including electrostatic interactions, van der Waals forces, and hydrophobic interactions (Banani *et al.*, 2017). Phase-separated condensates exhibit dynamic and reversible properties, allowing for rapid assembly and disassembly in response to changing environmental cues or developmental signals. The phase behavior of a protein is affected by various factors, such as intrinsic properties determined

New Phytologist

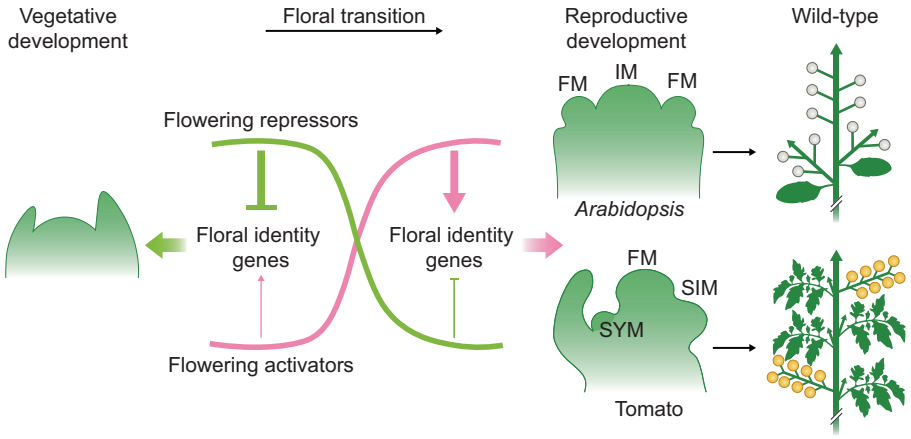

Fig. 1 The floral transition is associated with flowering time and inflorescence architecture in plants. Flowering repressors inhibit the expression of floral identity genes and maintain vegetative development; flowering activators induce the expression of these same genes and initiate reproductive development. This equilibrium ensures appropriate flowering time and inflorescence architecture in plants. FM, floral meristem; IM, inflorescence meristem; SIM, sympodial inflorescence meristem; SYM, sympodial meristem. The green blunt arrows indicate repression, the pink standard arrows indicate activation, the green standard arrows indicate main stems and canonical axillary shoots, and the gradient or black arrows indicate developmental directions.

by its amino acid sequence, posttranslational modifications, interaction partners, and the cellular environment. Notably, intrinsically disordered regions (IDRs), which encompass prion-like domains (PrDs) or low-complexity sequences with a biased amino acid composition, and specific domains such as coiled-coil and SH2 domains can promote multivalent interactions with proteins or nucleic acids to trigger phase separation (Alberti *et al.*, 2019; Zhu *et al.*, 2020, 2021).

Floral transition

In flowering plants, flowering time and inflorescence architecture of plants are determined by the floral transition after a programmed maturation process of the shoot apical meristem (SAM). Before floral transition, despite expansion and doming (Park *et al.*, 2012; Tal *et al.*, 2017; Kinoshita *et al.*, 2020), the SAM remains in a vegetative state due to the higher activity of flowering repressors (Fig. 1), such as FLOWERING LOCUS C (FLC) in Arabidopsis and TERMINATING FLOWER (TMF) in tomato. FLC, a MADS-box transcription factor, directly represses the expression of flowering genes such as *FLOWERING LOCUS T* (*FT*) and *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*) (Helliwell *et al.*, 2006). TMF, an ALOG (Arabidopsis LIGHT-SENSITIVE HYPOCOTYL 1, *Oryza* G1) family transcription factor, maintains vegetative development and inhibits precocious floral transition by directly repressing the expression of floral identity gene *ANNATHA* (*AN*) (MacAlister *et al.*, 2012; Huang *et al.*, 2021). Once the SAM reaches a certain developmental stage or is stimulated by specific environmental signals, activators act or repressors release inhibition, or both occur simultaneously to initiate the expression of floral identity genes (Fig. 1). For instance, leaf-derived florigen signals, including FT and FT orthologs, are transported to the SAM to induce the transition of vegetative meristems (VMs) to inflorescence meristems (IMs) that gives rise to floral meristems (FMs) (Park *et al.*, 2014; Tsuji & Sato, 2024). This process is controlled by the spatiotemporal expression of a group of floral identity genes, such as *APETALA1* (*API*), *FRUITFULL* (*FUL*), *UNUSUAL FLORAL ORGANS* (*UFO*), and *LEAFY* (*LFY*), which are regulated by both florigen-dependent and florigen-independent pathways (MacAlister *et al.*, 2012; Leijten *et al.*, 2018; Meir *et al.*, 2021; Nguyen & Gutzat, 2022; Shi & Vernoux, 2022).

The discovery and elucidation of the biomolecular condensation mechanisms of biomacromolecules have significantly enhanced our understanding of floral transition regulated by both pathways. Here, we focus on recent advances in biomolecular condensation regulated floral transition (Table 1).

II. Biomolecular condensation promotes floral transition by repressing *FLC*

The flowering repressor FLC plays a central role in both autonomous and vernalization pathways for the regulation of floral transition in Arabidopsis. Recent studies have shown that biomolecular condensation promotes floral transition by repressing the initiation of *FLC* transcription and elongation of *FLC* transcripts (Fig. 2a).

FLC regulation in the autonomous pathway

The autonomous pathway promotes flowering independent of day length. It includes RNA-binding proteins, RNA 3′ end processing factors, and chromatin modifiers, all of which work together to repress *FLC* expression (Wu *et al.*, 2020). First, FLOWERING CONTROL LOCUS A (FCA) condensates repress *FLC* transcription by increasing polyadenylation of the antisense transcript *COOLAIR*. FCA, an RNA-binding protein involved in flowering, interacts with an RNA 3′ end processing factor, FY, to promote the proximal polyadenylation of *COOLAIR*, which is transcribed from the *FLC* locus, triggering the chromatin silencing of *FLC* (Simpson *et al.*, 2003; Liu *et al.*, 2010). FCA contains two PrDs and undergoes phase separation to form nuclear bodies in a manner dependent on the coiled-coil protein FLC EXPRESSOR-LIKE 2 (FLL2). Like FCA, FLL2 also exhibits PrD-dependent phase separation properties, which are essential for FCA function (Fang *et al.*, 2019). The FCA nuclear bodies colocalize with and compartmentalize another RNA-binding protein, FPA, and the RNA 3′ end-processing factor FY, to enhance polyadenylation of *COOLAIR*, thereby repressing *FLC* transcription (Fang *et al.*, 2019).

Table 1 Proteins involved in floral transition by phase separation.

Protein name	Activity in condensates	Function of the condensates in floral transition	Reference
VRN1	Activated	Promotion	Zhou *et al*. (2019)
EMB1579	Activated	Promotion	Zhang *et al*. (2020)
DCP5/SSF	Activated	Promotion	Wang *et al*. (2023)
FRI	Repressed	Promotion	Zhu *et al*. (2021)
HRLP/SR45	Activated	Promotion	Zhang *et al*. (2022)
FCA/FLL2	Activated	Promotion	Fang *et al*. (2019)
TMF	Activated	Inhibition	Huang *et al*. (2021)
TFAM1/2/3/11	Activated	Inhibition	Huang *et al*. (2022)
phyB	Activated	Inhibition	Chen *et al*. (2022)
CRY2	Activated	Promotion	Wang *et al*. (2021)
ELF3	Repressed	Promotion	Jung *et al*. (2020)
ECT2/3/4	Activated	Promotion	Lee *et al*. (2022)
EHD6	Activated	Promotion	Cui *et al*. (2024)

CRY2, cryptochrome2; DCP5, DECAPPING 5; ECT, EVOLUTIONARILY CONSERVED C-TERMINAL REGION; EHD6, EARLY HEADING DATE6; ELF3, EARLY FLOWERING3; EMB1579, EMBRYO DEFECTIVE 1579; FCA, FLOWERING CONTROL LOCUS A; FLL2, FLC EXPRESSOR-LIKE 2; FRI, FRIGIDA; HRLP, HETEROGENEOUS NUCLEAR RIBONUCLEOPROTEIN R-LIKE PROTEIN; phyB, phytochrome B; SR45, SERINE/ARGININE-RICH 45; SSF, SISTER OF FCA; TFAM, TMF FAMILY MEMBERs; TMF, TERMINATING FLOWER; VRN1, VERNALIZATION1.

Second, HETEROGENEOUS NUCLEAR RIBONUCLEOPROTEIN R-LIKE PROTEIN (HRLP) condensates repress *FLC* transcription by sequestering polymerase II (Pol II). HRLP, an RNA-binding protein, interacts with the splicing factor SERINE/ARGININE-RICH 45 (SR45) to form nuclear bodies via LLPS. HRLP–SR45 condensates compartmentalize RNA Pol II and decrease its enrichment over the region near intron I of *FLC*, thereby increasing the R-loop (DNA:RNA hybrid) level at the *FLC* locus (Zhang *et al*., 2022). Additionally, Pol II enrichment at the *FLC* locus is also inhibited by the nuclear condensate formed by PrD-mediated LLPS of DECAPPING 5 (DCP5), a P-body component, and the scaffold protein SISTER OF FCA (SSF), an interacting partner of DCP5 (Wang *et al*., 2023). These condensates sequester Pol II and fine-tune *FLC* transcription, thereby promoting the floral transition in Arabidopsis.

FLC regulation during vernalization

Vernalization induces the floral transition after overwintering by epigenetically silencing *FLC* expression in Arabidopsis. Biomolecular condensation enhances chromatin silencing of the *FLC* locus by promoting the activity of repressors. VERNALIZATION1 (VRN1) acts together with vernalization-specific transcription factors to repress *FLC* expression (Levy *et al*., 2002). Additionally, VRN1 is essential for the epigenetic regulation of *FLC* (Bastow *et al*., 2004). VRN1 can bind to DNA sequences from the *FLC* promoter and undergo LLPS *in vitro*, depending on its B3 domains linked by an IDR (Zhou *et al*., 2019). VRN1 may recruit epigenetic and transcriptional factors by forming condensates to control *FLC* silencing in response to prolonged cold exposure.

The plant-specific EMBRYO DEFECTIVE 1579 (EMB1579) condensates repress *FLC* expression by binding to the *FLC* genomic sequence. EMB1579 contains IDRs enriched in hydrophobic amino acids and undergoes phase separation to form liquid-like condensates in the nucleus. EMB1579 condensates interact with MULTIPLE SUPPRESSOR OF IRA 4 (MSI4) and condense the CUL4–DDB1^{MSI4} complex, which consists of MSI4, DNA DAMAGE BINDING PROTEIN 1 (DDB1), and Cullin 4 (CUL4), thereby promoting H3K27 trimethylation at the *FLC* locus and repressing its transcription (Zhang *et al*., 2020).

FRIGIDA (FRI), a nuclear protein with two coiled-coil regions, is an important determinant of the vernalization response in early cold phase. Diffused FRI interacts with other *FLC*-specific regulators to form a complex that recruits general transcription factors and chromatin modification factors to activate *FLC* transcription (Geraldo *et al*., 2009; Choi *et al*., 2011). Cold temperatures promote the formation of FRI nuclear condensates via its two coiled-coil regions and C-terminal IDR (Zhu *et al*., 2021). FRI condensation sequesters FRI complex and reduces its occupancy at the *FLC* promoter and thus *FLC* transcription, which is dynamic, allowing for reversible changes in FLC expression to monitor seasonal progression and initiate floral transition at favorable times (Zhu *et al*., 2021). This regulation differs from the vernalization memory controlled by Polycomb nucleation, a more stable and heritable state, ensuring that *FLC* remains silenced after the plant has experienced sufficient cold.

III. Biomolecular condensation programs floral transition via a florigen-independent pathway

Biomolecular condensation of transcription factors has been found to programs floral transition by maintaining vegetative development of shoot meristems. In tomato, the loss-of-function of *TMF* accelerates floral transition independently of florigen, leading to early flowering and single-flowered primary inflorescences (MacAlister *et al*., 2012). TMF interacts with transcriptional cofactors BLADE-ON-PETIOLE (BOPs) in the nucleus to ensure progressive meristem maturation and control inflorescence architecture in tomato (Xu *et al*., 2016). TMF harbors two typical

New Phytologist

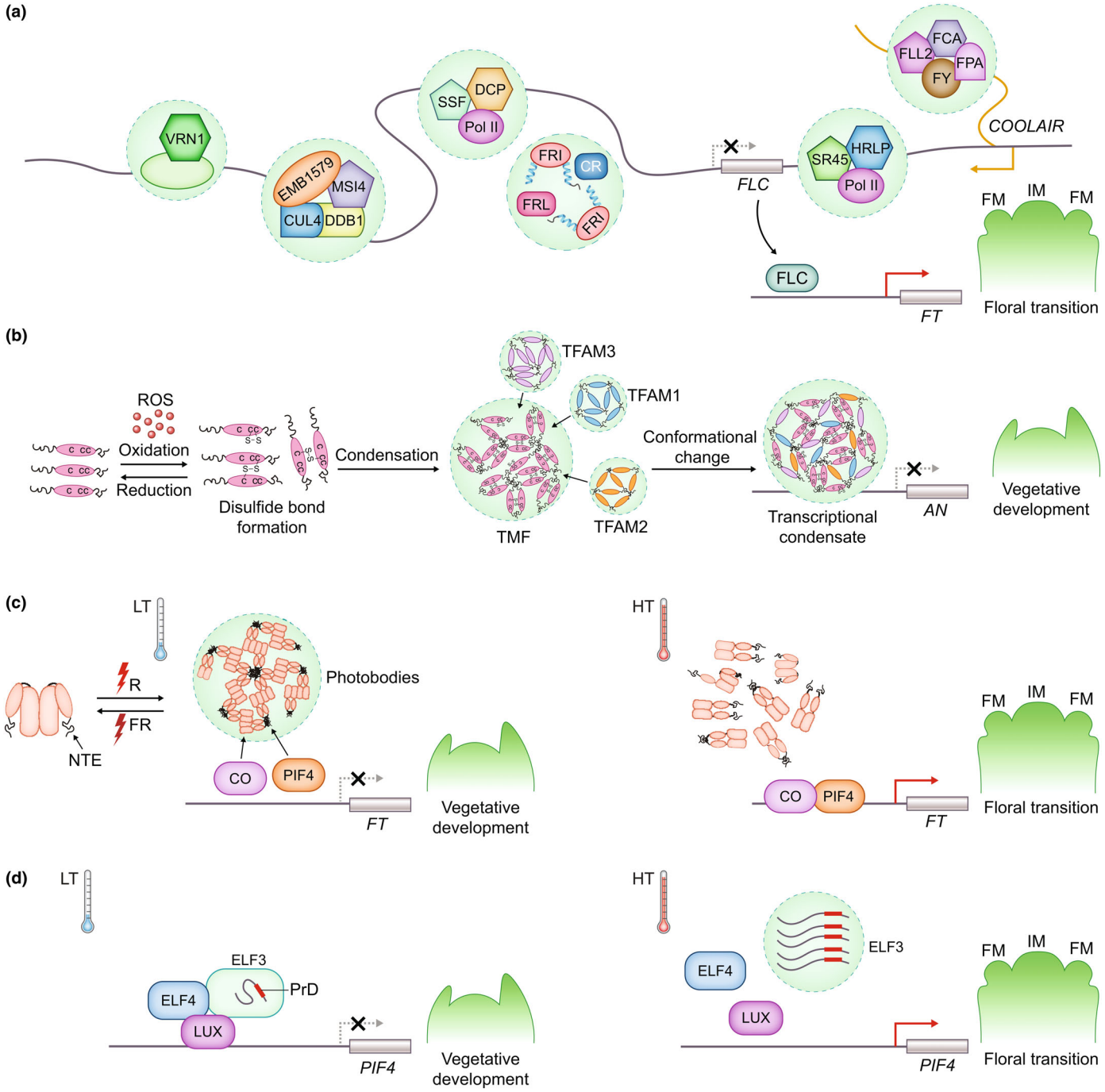

Fig. 2 Biomolecular condensates integrate developmental and environmental signals to regulate the floral transition in plants. (a) Biomolecular condensates repress *FLC* transcription to promote Arabidopsis floral transition. (b) Heterotypic transcriptional condensates formed by TMF and TFAMs maintain vegetative development of the SAM in tomato. (c) Low temperature-induced phyB condensates repress floral transition by sequestering flowering activators. (d) High temperature-induced ELF3 condensates promote the floral transition by derepressing flowering activators. Biomolecular condensates are represented as dashed circles. *AN*, *ANNATHA*; C, cysteine residue; CO, CONSTANS; CR, cotranscriptional regulators; CUL4, Cullin 4; DCP5, DECAPPING 5; DDB1, DNA DAMAGE BINDING PROTEIN 1; ELF3, EARLY FLOWERING3; ELF4, EARLY FLOWERING 4; EMB1579, EMBRYO DEFECTIVE 1579; FCA, FLOWERING CONTROL LOCUS A; *FLC*, *FLOWERING LOCUS C*; FLL2, FLC EXPRESSOR-LIKE 2; FM, floral meristem; FR, far-red light; FRI, FRIGIDA; FRL, FRIGIDA-LIKE; *FT*, *FLOWERING LOCUS T*; HRLP, HETEROGENEOUS NUCLEAR RIBONUCLEOPROTEIN R-LIKE PROTEIN; HT, high temperature; IM, inflorescence meristem; LT, low temperature; LUX, LUX ARRHYTHMO; MSI4, MULTIPLE SUPPRESSOR OF IRA 4; NTE, N-terminal extension; PIF4, PHYTOCHROME-INTERACTING FACTOR 4; Pol II, polymerase II; PrD, prion-like domain; R, red light; ROS, reactive oxygen species; S, sulfhydryl; SR45, SERINE/ARGININE-RICH 45; SSF, SISTER OF FCA; TFAM, TMF FAMILY MEMBERs; TMF, TERMINATING FLOWER; VRN1, VERNALIZATION1.

prion-like IDRs, one at the N-terminus and the other at the C-terminus. A recent study revealed that TMF can sense the developmentally produced reactive oxygen species (ROS) in the peripheral regions of the SAM to form disulfide bonds, triggering LLPS to form condensates (Fig. 2b; Huang *et al.*, 2021).

ALOG family in tomato comprises 12 members called TMF FAMILY MEMBERs (TFAMs) (MacAlister *et al.*, 2012). Like *TMF*, the *TFAM1*, *TFAM2*, *TFAM3* and *TFAM11* are expressed at different vegetative stages of SAM and encode proteins with typical prion-like IDRs at the N- and/or C-terminus, which also undergo phase separation. Genetic variations in the IDRs of TMF and TFAMs derived from genome duplication results in different capacities to form liquid-like droplets (Huang *et al.*, 2022). The heterotypic interaction and phase separation of TMF and TFAMs promote protein complex rewiring to form robust transcriptional condensates that directly bind to the promoter of the floral identity gene *AN* and precisely control its expression (Fig. 2b). The heterotypic transcriptional condensates formed by different ALOG family members canalize shoot meristem maturation program to ensure the timing of flowering and the establishment of inflorescence architecture in tomato (Huang *et al.*, 2021, 2022). Accordingly, plants with different combination of mutations in *TMF* and *TFAM*s showed a continuum of flowering times, ranging from normal to exceptionally early. Correspondingly, their inflorescence architectures varied from multiple flowers to a singular flower (Huang *et al.*, 2018, 2022). Interestingly, the intensity of phenotypes observed in single mutants of *tmf* or *tfam* mutants was notably correlated with the phase separation capacity of the proteins encoded by the responsible genes. These studies revealed the role of biomolecular condensation in assembling multiple proteins into a transcriptional condensates to achieve a robust control of programmed maturation of shoot meristems and thus determine flowering time and inflorescence architecture.

IV. Biomolecular condensation integrates environmental signals to regulate floral transition

The dynamic fluctuations of light and temperature allow plants to sense seasonal changes and adjust their developmental transitions (Casal & Qüesta, 2018). As sessile organisms, plants integrate environmental signals to initiate their floral transition at the optimal time. Several studies have demonstrated that environmental signals trigger biomolecular condensation to regulate floral transition.

In plant photomorphogenesis, the cryptochrome (CRY1 and CRY2, blue light receptors) and phytochrome B (phyB, red and far-red receptor) form photobodies and antagonistically regulate floral transition by oppositely regulating the flowering activator CONSTANS (CO) in Arabidopsis (Su *et al.*, 2017). CRY2 undergoes blue light-dependent phosphorylation and LLPS to form photobodies, promoting the floral transition (Liu *et al.*, 2017; Wang *et al.*, 2021). In addition to blue light regulated photobodies, red light can change phyB protein conformation by promoting the conversion from its inactive far-red light-absorbing (Pr) form to the active red light-absorbing (Pfr) form, which undergoes LLPS to form phyB condensates via its N-terminal extension (NTE), a phase-separating IDR (Chen *et al.*, 2022). Red light-activated phyB can recruit its interacting proteins such as PHYTOCHROME-INTERACTING FACTOR 4 (PIF4) into condensates (Chen *et al.*, 2022). PIF4 is a basic helix–loop–helix (bHLH) transcription factor that can bind to the *FT* promoter and promote its expression to positively regulate high temperature-induced early flowering in Arabidopsis (Kumar *et al.*, 2012). Additionally, phyB has the ability to sense temperature signals. Specifically, low temperatures induce the formation of phyB condensates, and high temperatures induce Pfr-to-Pr reversion and abolition of phyB condensates (Legris *et al.*, 2016; Chen *et al.*, 2022). Since *phyb* mutants exhibit early flowering (Reed *et al.*, 1993), we speculate that phyB condensates may maintain vegetative development by sequestering flowering activators to reduce their binding to the *FT* promoter. High temperature abolish phyB condensate, releasing flowering activators that promote *FT* expression, thereby accelerating floral transition (Fig. 2c). Temperature and light always work together to control the floral transition in plants. The condensation of phyB reveals a strategy that simultaneously integrates different environmental signals to regulate development.

In contrast to phyB, increasing temperature induces the condensation of the PrD-containing protein EARLY FLOWERING 3 (ELF3), a core component of the circadian evening complex (Nusinow *et al.*, 2011; Jung *et al.*, 2020). Under low temperatures, the evening complex formed by diffuse ELF3, ELF4, and LUX ARRHYTHMO (LUX) acts as a transcriptional repressor to inhibit the expression of genes that promote floral transition, such as *PIF4*, maintaining vegetative development in Arabidopsis (Nusinow *et al.*, 2011; Kumar *et al.*, 2012; Jung *et al.*, 2020). Increasing temperatures induce the assembly of ELF3 condensates, which dissociates the evening complex, thus lowering its locus occupancy and transcriptional repression of target genes and promoting floral transition (Fig. 2d).

V. Conclusions and perspectives

Floral transition not only determines plant diversity but also affects the harvesting time and final yield of crops. A delayed or accelerated transition to flowering may result in plants that are poorly adapted to their environment, leading to substantial yield losses. Therefore, the abundance and molecular status of floral transition regulators must be dynamically balanced to ensure a precise and flexible transitional program. Biomolecular condensate, featured by reversible assembly and relatively isolated microenvironment, acts as an organizer for complex regulation by compartmentalizing cellular reactions and plays a critical role in the dynamic coordination of regulators and signals involved in floral transition.

The occurrence, capacity, and duration of biomolecular condensates represent different parameters to quantify their functions, and these distinct properties may be reflected by traceable and quantitative changes in cellular activities or phenotypes. Flowering time and inflorescence architecture are easily quantified and influenced by gene dosage. Engineering biomolecular condensation of flowering regulators holds promise for creating quantitative traits related to flowering time and

inflorescence structure. Supporting this, natural variations in ELF3 alter the capacity of phase separation, affecting the temperature adaptability of floral transition in different species (Jung *et al.*, 2020). The IDR and cysteine-mediated phase separation of TMF and TFAM proteins controls the floral transition, thereby influencing flowering time and inflorescence architecture in tomato (Huang *et al.*, 2021, 2022). Moreover, variations in IDRs of the TMF and TFAM proteins leads to different phase separation capacity that correlates with their functional significance in the regulation of floral transition (Huang *et al.*, 2022). The sequence variations of the aforementioned genes, along with the diversity of mechanisms for the formation and regulation of biomolecular condensates, provide insights for the rational design of desirable biomolecular condensates.

De novo engineering of condensates has been demonstrated in prokaryotic and eukaryotic cells by utilizing modular domains, such as IDRs or multivalent interaction motifs, to control the properties and behavior of condensates (Bracha *et al.*, 2019; Dzuricky *et al.*, 2020; Reinkemeier & Lemke, 2021; Lasker *et al.*, 2022). If this strategy is applied to plants, particularly to major crops, it is likely to generate new phenotypic variations and confer greater developmental plasticity and stress resilience to these crops. This holds significant potential for future agriculture in mitigating crop yield loss caused by global climate change.

Acknowledgements

This research was supported by the grants from National Natural Science Foundation of China (no. 32225045) and the Youth Innovation Promotion Association of the Chinese Academy of Sciences (no. 2022094).

Competing interests

None declared.

Author contributions

CX designed and supervised the paper; XH wrote the paper with the help of YY; CX revised the manuscript.

ORCID

Cao Xu https://orcid.org/0000-0002-9055-7691

References

Alberti S, Gladfelter A, Mittag T. 2019. Considerations and challenges in studying liquid-liquid phase separation and biomolecular condensates. *Cell* **176**: 419–434.

Banani SF, Lee HO, Hyman AA, Rosen MK. 2017. Biomolecular condensates: organizers of cellular biochemistry. *Nature Reviews Molecular Cell Biology* **18**: 285–298.

Bastow R, Mylne JS, Lister C, Lippman Z, Martienssen RA, Dean C. 2004. Vernalization requires epigenetic silencing of *FLC* by histone methylation. *Nature* **427**: 164–167.

Boeynaems S, Alberti S, Fawzi NL, Mittag T, Polymenidou M, Rousseau F, Schymkowitz J, Shorter J, Wolozin B, Van Den Bosch L *et al.* 2018. Protein phase separation: a new phase in cell biology. *Trends in Cell Biology* **28**: 420–435.

Bracha D, Walls MT, Brangwynne CP. 2019. Probing and engineering liquid-phase organelles. *Nature Biotechnology* **37**: 1435–1445.

Casal JJ, Qüesta JI. 2018. Light and temperature cues: multitasking receptors and transcriptional integrators. *New Phytologist* **217**: 1029–1034.

Chen D, Lyu M, Kou XX, Li J, Yang ZX, Gao LL, Li Y, Fan LM, Shi H, Zhong SW. 2022. Integration of light and temperature sensing by liquid-liquid phase separation of phytochrome B. *Molecular Cell* **82**: 3015–3029.

Choi K, Kim J, Hwang HJ, Kim S, Park C, Kim SY, Lee I. 2011. The FRIGIDA complex activates transcription of *FLC*, a strong flowering repressor in *Arabidopsis*, by recruiting chromatin modification factors. *Plant Cell* **23**: 289–303.

Cui S, Song P, Wang C, Chen S, Hao B, Xu Z, Cai L, Chen X, Zhu S, Gan X *et al.* 2024. The RNA binding protein EHD6 recruits the m^6A reader YTH07 and sequesters OsCOL4 mRNA into phase-separated ribonucleoprotein condensates to promote rice flowering. *Molecular Plant* **17**: 935–954.

Dzuricky M, Rogers BA, Shahid A, Cremer PS, Chilkoti A. 2020. *De novo* engineering of intracellular condensates using artificial disordered proteins. *Nature Chemistry* **12**: 814–825.

Fang XF, Wang L, Ishikawa R, Li YX, Fiedler M, Liu FQ, Calder G, Rowan B, Weigel D, Li PL *et al.* 2019. FLL2 promotes liquid-liquid phase separation of polyadenylation complexes. *Nature* **569**: 265–269.

Geraldo N, Bäurle I, Kidou S, Hu XY, Dean C. 2009. FRIGIDA delays flowering in Arabidopsis via a cotranscriptional mechanism involving direct interaction with the nuclear cap-binding complex. *Plant Physiology* **150**: 1611–1618.

Helliwell CA, Wood CC, Robertson M, Peacock WJ, Dennis ES. 2006. 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* **46**: 183–192.

Huang XZ, Chen SD, Li WP, Tang LL, Zhang YQ, Yang N, Zou YP, Zhai XW, Xiao N, Liu W *et al.* 2021. ROS regulated reversible protein phase separation synchronizes plant flowering. *Nature Chemical Biology* **17**: 549–557.

Huang XZ, Tang LL, Yu Y, Dalrymple J, Lippman ZB, Xu C. 2018. Control of flowering and inflorescence architecture in tomato by synergistic interactions between ALOG transcription factors. *Journal of Genetics and Genomics* **45**: 557–560.

Huang XZ, Xiao N, Zou YP, Xie Y, Tang LL, Zhang YQ, Yu Y, Li YT, Xu C. 2022. Heterotypic transcriptional condensates formed by prion-like paralogous proteins canalize flowering transition in tomato. *Genome Biology* **23**: 78.

Jung JH, Barbosa AD, Hutin S, Kumita JR, Gao M, Derwort D, Silva CS, Lai X, Pierre E, Geng F *et al.* 2020. A prion-like domain in ELF3 functions as a thermosensor in Arabidopsis. *Nature* **585**: 256–260.

Kinoshita A, Vayssieres A, Richter R, Sang Q, Roggen A, van Driel AD, Smith RS, Coupland G. 2020. Regulation of shoot meristem shape by photoperiodic signaling and phytohormones during floral induction of Arabidopsis. *eLife* **9**: e60661.

Kumar SV, Lucyshyn D, Jaeger KE, Alós E, Alvey E, Harberd NP, Wigge PA. 2012. Transcription factor PIF4 controls the thermosensory activation of flowering. *Nature* **484**: 242–245.

Lasker K, Boeynaems S, Lam V, Scholl D, Stainton E, Briner A, Jacquemyn M, Daelemans D, Deniz A, Villa E *et al.* 2022. The material properties of a bacterial-derived biomolecular condensate tune biological function in natural and synthetic systems. *Nature Communications* **13**: 5643.

Lee HG, Kim J, Seo PJ. 2022. N^6-methyladenosine-modified RNA acts as a molecular glue that drives liquid-liquid phase separation in plants. *Plant Signaling & Behavior* **17**: 2079308.

Legris M, Klose C, Burgie ES, Rojas CCR, Neme M, Hiltbrunner A, Wigge PA, Schäfer E, Vierstra RD, Casal JJ. 2016. Phytochrome B integrates light and temperature signals in *Arabidopsis*. *Science* **354**: 897–900.

Leijten W, Koes R, Roobeek I, Frugis G. 2018. Translating flowering time from *Arabidopsis thaliana* to Brassicaceae and Asteraceae crop species. *Plants* **7**: 111.

Levy YY, Mesnage S, Mylne JS, Gendall AR, Dean C. 2002. Multiple roles of *Arabidopsis* VRN1 in vernalization and flowering time control. *Science* **297**: 243–246.

Liu F, Marquardt S, Lister C, Swiezewski S, Dean C. 2010. Targeted 3′ processing of antisense transcripts triggers Arabidopsis FLC chromatin silencing. *Science* **327**: 94–97.

Liu Q, Wang Q, Deng WX, Wang X, Piao MX, Cai DW, Li YX, Barshop WD, Yu XL, Zhou TT *et al.* 2017. Molecular basis for blue light-dependent phosphorylation of cryptochrome 2. *Nature Communications* **8**: 15234.

MacAlister CA, Park SJ, Jiang K, Marcel F, Bendahmane A, Izkovich Y, Eshed Y, Lippman ZB. 2012. Synchronization of the flowering transition by the tomato gene. *Nature Genetics* **44**: 1393–1398.

Meir Z, Aviezer I, Chongloi GL, Ben-Kiki O, Bronstein R, Mukamel Z, Keren-Shaul H, Jaitin D, Tal L, Shalev-Schlosser G *et al.* 2021. Dissection of floral transition by single-meristem transcriptomes at high temporal resolution. *Nature Plants* **7**: 800–813.

Nguyen V, Gutzat R. 2022. Epigenetic regulation in the shoot apical meristem. *Current Opinion in Plant Biology* **69**: 102267.

Nusinow DA, Helfer A, Hamilton EE, King JJ, Imaizumi T, Schultz TF, Farre EM, Kay SA. 2011. The ELF4-ELF3-LUX complex links the circadian clock to diurnal control of hypocotyl growth. *Nature* **475**: 398–402.

Park SJ, Eshed Y, Lippman ZB. 2014. Meristem maturation and inflorescence architecture – lessons from the Solanaceae. *Current Opinion in Plant Biology* **17**: 70–77.

Park SJ, Jiang K, Schatz MC, Lippman ZB. 2012. Rate of meristem maturation determines inflorescence architecture in tomato. *Proceedings of the National Academy of Sciences, USA* **109**: 639–644.

Reed JW, Nagpal P, Poole DS, Furuya M, Chory J. 1993. Mutations in the gene for the red far-red light receptor phytochrome-B alter cell elongation and physiological-responses throughout Arabidopsis development. *Plant Cell* **5**: 147–157.

Reinkemeier CD, Lemke EA. 2021. Synthetic biomolecular condensates to engineer eukaryotic cells. *Current Opinion in Chemical Biology* **64**: 174–181.

Shi BH, Vernoux T. 2022. Hormonal control of cell identity and growth in the shoot apical meristem. *Current Opinion in Plant Biology* **65**: 102111.

Simpson GG, Dijkwel PP, Quesada V, Henderson I, Dean C. 2003. FY is an RNA 3′ end-processing factor that interacts with FCA to control the *Arabidopsis* floral transition. *Cell* **113**: 777–787.

Su J, Liu BB, Liao JK, Yang ZH, Lin CT, Oka Y. 2017. Coordination of cryptochrome and phytochrome signals in the regulation of plant light responses. *Agronomy* **7**: 25.

Tal L, Friedlander G, Gilboa NS, Unger T, Gilad S, Eshed Y. 2017. Coordination of meristem doming and the floral transition by late termination, a kelch repeat protein. *Plant Cell* **29**: 681–696.

Tsuji H, Sato M. 2024. The function of florigen in the vegetative-to-reproductive phase transition in and around the shoot apical meristem. *Plant and Cell Physiology* **65**: 322–337.

Wang WY, Wang CH, Wang YH, Ma J, Wang TY, Tao Z, Liu PP, Li S, Hu YY, Gu AJ *et al.* 2023. The P-body component DECAPPING5 and the floral repressor SISTER OF FCA regulate *FLOWERING LOCUS C* transcription in Arabidopsis. *Plant Cell* **35**: 3303–3324.

Wang X, Jiang BC, Gu LF, Chen YD, Mora M, Zhu M, Noory E, Wang Q, Lin CT. 2021. A photoregulatory mechanism of the circadian clock in *Arabidopsis*. *Nature Plants* **7**: 1397–1408.

Wu Z, Fang XF, Zhu DL, Deati C. 2020. Autonomous pathway: FLOWERING LOCUS C repression through an antisense-mediated chromatin-silencing mechanism. *Plant Physiology* **182**: 27–37.

Xu C, Park SJ, Van Eck J, Lippman ZB. 2016. Control of inflorescence architecture in tomato by BTB/POZ transcriptional regulators. *Genes & Development* **30**: 2048–2061.

Zhang Y, Fan S, Hua CM, Teo ZWN, Kiang JX, Shen LS, Yu H. 2022. Phase separation of HRLP regulates flowering time in *Arabidopsis*. *Science Advances* **8**: eabn5488.

Zhang YL, Li ZK, Chen NZ, Huang Y, Huang SJ. 2020. Phase separation of Arabidopsis EMB1579 controls transcription, mRNA splicing, and development. *PLoS Biology* **18**: e3000782.

Zhou H, Song Z, Zhong S, Zuo L, Qi Z, Qu LJ, Lai L. 2019. Mechanism of DNA-induced phase separation for transcriptional repressor VRN1. *Angewandte Chemie International Edition* **58**: 4858–4862.

Zhu GY, Xie JJ, Kong WN, Xie JF, Li YC, Du L, Zheng QG, Sun L, Guan MF, Li H *et al.* 2020. Phase separation of disease-associated SHP2 mutants underlies MAPK hyperactivation. *Cell* **183**: 490–502.

Zhu P, Lister C, Dean C. 2021. Cold-induced *Arabidopsis* FRIGIDA nuclear condensates for *FLC* repression. *Nature* **599**: 657–661.