SOCIETY FOR EXPERIMENTAL BIOLOGY

Journal of Experimental Botany
https://doi.org/10.1093/jxb/erae112 Advance Access Publication 12 March 2024

REVIEW PAPER

Flowering time genes branching out

Pierangela E. Colleoni[1], Sam W. van Es[1,2,†], Ton Winkelmolen[1], Richard G. H. Immink[1,2], and G. Wilma van Esse[1,*]

[1] Laboratory of Molecular Biology, Wageningen University and Research, 6708 PB, Wageningen, The Netherlands
[2] Bioscience, Wageningen Plant Research, Wageningen University and Research, 6708 PB, Wageningen, The Netherlands
[†] Present address: Department of Plant Biology, Linnean Centre for Plant Biology, Swedish University of Agricultural Sciences (SLU), Uppsala 75007, Sweden

* Correspondence: wilma.vanesse@wur.nl

Received 29 November 2023; Editorial decision 6 March 2024; Accepted 11 March 2024

Editor: Pablo Manavella, Instituto de Agrobiotecnología del Litoral, Argentina

Abstract

Plants are sessile by nature, and as such they have evolved to sense changes in seasonality and their surrounding environment, and adapt to these changes. One prime example of this is the regulation of flowering time in angiosperms, which is precisely timed by the coordinated action of two proteins: FLOWERING LOCUS T (FT) and TERMINAL FLOWER 1 (TFL1). Both of these regulators are members of the PHOSPHATIDYLETHANOLAMINE BINDING PROTEIN (PEBP) family of proteins. These regulatory proteins do not interact with DNA themselves, but instead interact with transcriptional regulators, such as FLOWERING LOCUS D (FD). FT and TFL1 were initially identified as key regulators of flowering time, acting through binding with FD; however, PEBP family members are also involved in shaping plant architecture and development. In addition, PEBPs can interact with TCP transcriptional regulators, such as TEOSINTE BRANCHED 1 (TB1), a well-known regulator of plant architecture, and key domestication-related genes in many crops. Here, we review the role of PEBPs in flowering time, plant architecture, and development. As these are also key yield-related traits, we highlight examples from the model plant Arabidopsis as well as important food and feed crops such as, rice, barley, wheat, tomato, and potato.

Keywords: Architecture, branching, flowering, *FLOWERING LOCUS T*, *TEOSINTE BRANCHED 1*, transcription factors.

Introduction

A huge variation in appearance exists within the plant kingdom, even between plants of the same species. An underlying reason for this is that plants are sessile organisms and need a huge degree of plasticity to survive less favourable conditions. Plants therefore respond to subtle differences in their environment. This also holds true for the regulation of flowering time in angiosperms. Here, plants respond to signals such as increasing day length and temperature to sense the optimal time to switch from vegetative to reproductive growth.

Rice (*Oryza sativa*), barley (*Hordeum vulgare*), and wheat (*Triticum aestivum*) are monocotyledons belonging to the *Poaceae* family, commonly known as grasses. With a total cultivated area of over 4 million km^2 in 2021 (Food and Agriculture Organization of the United Nations, 2023), they represent

staples for the entire world population. Rice was domesticated in southern China (Huang *et al.*, 2012). It is a facultative short-day (SD) plant, which accelerates flowering under short days but is also able to flower under non-inductive long-day (LD) conditions. Nowadays, rice is cultivated at a greater range of latitudes across the globe, thanks to the selection of photoperiod-insensitive varieties (Gómez-Ariza *et al.*, 2015; Zong *et al.*, 2021). Barley and wheat, on the other hand, are temperate cereals mainly domesticated in the Fertile Crescent (Morrell and Clegg, 2007; Peleg *et al.*, 2011; Poets *et al.*, 2015; Pankin *et al.*, 2018; Zhao *et al.*, 2023). For both of these species, two different growth types have been selected during domestication, based on the presence of a vernalization requirement or on sensitivity/insensitivity to photoperiod for the initiation of flowering (reviewed in Fernández-Calleja *et al.*, 2021). 'Winter' varieties need to satisfy a vernalization requirement to initiate reproductive development. Conversely, 'spring' varieties are able to flower irrespective of vernalization. Independently, varieties can be photoperiod-sensitive or -insensitive; photoperiod-sensitive plants are characterized by accelerated flowering under LD conditions. The architecture of the vegetative shoot of rice, barley, and wheat is similar, with leaves produced from the main shoot apical meristem (SAM) in a distichous phyllotaxis, subtending axillary buds that may or may not develop into secondary shoots known as tillers. Inflorescence architecture, on the other hand, is extremely diverse among cereals (Bommert *et al.*, 2005; Bommert and Whipple, 2018). Similarly, a high diversity in architecture and development can be observed in the dicotyledonous family of the *Solanaceae*, to which both tomato (*Solanum lycopersicum*) and potato (*Solanum tuberosum*) belong. Both originally domesticated in the Andean region (Spooner *et al.*, 2005; Bai and Lindhout, 2007), these species represent an important source of food and feed, with nearly 200 tonnes and 499 million tonnes, respectively, produced in 2021 (Food and Agriculture Organization of the United Nations, 2023). Tomato is a day-neutral plant that presents a sympodial growth habit. Upon floral initiation, the primary shoot transitions to a reproductive state, leading to the formation of a first inflorescence. The onset of the inflorescence does not coincide with the termination of shoot growth. Instead, shoot growth continues from the outgrowth of the last axillary meristem produced before transition, the so-called sympodial meristem (SYM). After the production of a few leaves, the sympodial meristem also transitions to an inflorescence meristem, and shoot growth is taken over by the last SYM produced. This repetitive pattern is continued until exhaustion, and shapes the architecture of both tomato shoot and inflorescence (reviewed in Périlleux and Huerga-Fernández, 2022). Potato plants can reproduce both sexually and asexually, through the formation of flowers and tubers, respectively. Tubers are storage organs derived from the swelling of stolons, a special type of underground stems. The induction of tuber formation is strongly dependent on environmental cues. Wild potato (*Solanum tuberosum* ssp. *andigena*) forms tubers under SD conditions (Jackson, 1999), whereas modern varieties (*Solanum tuberosum* ssp. *tuberosum*) have been bred to induce tuber formation under LD conditions (reviewed in Rodríguez-Falcón *et al.*, 2006). Little is known about the most favourable conditions for potato flowering, but it has been demonstrated that the process is inhibited during tuber formation (Plantenga *et al.*, 2016, 2019).

There is a vast difference in plant architecture, growth habit, and developmental timing between the above-mentioned species. However, the main players orchestrating plant architecture and developmental timing seem to be conserved. Flowering time is in all cases induced by FLOWERING LOCUS T (FT)-like proteins and relies on their interaction with FLOWERING LOCUS D (FD)-like proteins of the bZIP transcription factor family, while architecture is, under the control of conserved TCP proteins, among others. These two traits are tightly linked, and evidence suggests that the interplay between PHOSPHATIDYLETHANOLAMINE BINDING PROTEINs (PEBPs) and TCPs is not only critical in the coordination of plant growth, but also highly conserved across angiosperms. In this review we present an overview of the roles of *PEBPs*, *bZIPs*, and *TCPs* in the regulation of flowering time and plant architecture, and how the interaction between members of these gene families shapes the life cycle of both monocot and dicot crops.

Day length and temperature induce the expression of *FLOWERING LOCUS T*

Synchronizing the reproductive phase with the most favourable environmental conditions is crucial to maximize the plant's reproductive potential. To align the start of the reproductive phase with the environment, plants can sense different stimuli, such as day length (i.e. photoperiod) and temperature. Photoperiodic flowering relies on the components of the circadian clock and follows the external coincidence model (Pittendrigh and Minis, 1964). When the external light input coincides with a sensitive phase of an output of the circadian clock, flowering is initiated. Whether this happens under long days, short days, or both depends on the growth habit of the plant. In the model plant Arabidopsis, the floral regulators *GIGANTEA* (*GI*), *CONSTANS* (*CO*), and *FT* play key roles in the photoperiodic flowering responses (Mizoguchi *et al.*, 2005). This pathway is highly conserved in plants; however, minor differences may occur between species. In rice, for example, which is a facultative SD plant, two parallel photoperiodic pathways have been identified (recently reviewed in Vicentini *et al.*, 2023). One pathway is mediated by the rice homologue of *GIGANTEA* (*OsGI*), the *CONSTANS-like* gene *Heading date 1* (*Hd1*), and the *FT* orthologue *Hd3a*, which act analogously to the Arabidopsis *GI*, *CO*, and *FT* cascade (Hayama *et al.*, 2003). A second route that controls the expression of *Hd3a* in response to photoperiod depends on the rice-specific genes *Grain number, plant height and heading date* 7 (*Ghd7*), *Ghd8*, and

Early heading date 1 (*Ehd1*). This network also controls the expression of a second florigen, *RICE FLOWERING LOCUS T 1* (*RFT1*) (Doi *et al.*, 2004; Komiya *et al.*, 2009; Zhang *et al.*, 2015; Zong *et al.*, 2021). Under SD conditions, flowering is accelerated via the promotion of *Hd3a* and *RFT1* by *Hd1* and *Edh1* (Doi *et al.*, 2004; Zhang *et al.*, 2015). Under LD conditions, genetic and protein–protein interactions between *Hd1* and the LD flowering regulators *Ghd7*, *Ghd8*, and *PSEUDO-RESPONSE REGULATOR 37* (*OsPRR37*) inhibit *Hd3a* and *RFT1* expression (Goretti *et al.*, 2017; Cai *et al.*, 2019; Zhang *et al.*, 2019; Zong *et al.*, 2021; Sun *et al.*, 2022). The conversion of *Hd1* from an activator of flowering under SD conditions to a repressor of flowering under LD conditions is dependent on *PHYTOCHROME B* (*OsPHYB*) (Izawa *et al.*, 2002) and on the interacting partners Ghd7 and Ghd8 (Nemoto *et al.*, 2016; Du *et al.*, 2017; Goretti *et al.*, 2017; Zhang *et al.*, 2017; Zong *et al.*, 2021). Hd1 can form a complex with Ghd8 to silence *Hd3a* expression (Du *et al.*, 2017; Goretti *et al.*, 2017). In addition, Hd1 negatively regulates *Ehd1* expression by forming a complex with Ghd7, or with both Ghd7 and Ghd8 (Nemoto *et al.*, 2016; Zhang *et al.*, 2017; Zong *et al.*, 2021). *OsPRR37* also plays a key role in the control of photoperiodic flowering, as under long days, it down-regulates *Ehd1* expression, acting downstream of *OsPHYB* or via interaction with Ghd8 (Gao *et al.*, 2014; Goretti *et al.*, 2017). *OsMADS50* is an LD flowering promoter, acting upstream of *Ehd1* (Komiya *et al.*, 2009; Ryu *et al.*, 2009). As a result, flowering under long days is delayed compared with short days, and is exclusively promoted by *RFT1* (Komiya *et al.*, 2009; Giaume *et al.*, 2023).

Rice is a tropical plant and therefore does not need to experience a period of cold to start its reproductive phase. In contrast, in plants that are vernalization sensitive, such as winter accessions of barley and wheat, photoperiod-induced flowering is initiated only if a vernalization requirement is satisfied (recently reviewed in Dixon *et al.*, 2022). The crosstalk between the photoperiod (PPD) and vernalization (VRN) pathways happens at the *VERNALIZATION 1* (*VRN1*) and *VRN2* levels (Yan *et al.*, 2004; Turner *et al.*, 2013; Deng *et al.*, 2015). Before vernalization, *VRN2* inhibits *FT1* expression (Mulki and von Korff, 2016). After the vernalization requirement is satisfied, *VRN1* expression levels increase. VRN1 promotes *FT1* by directly binding to the *FT1* promoter (Deng *et al.*, 2015) and by lifting *VRN2*-mediated repression (Yan *et al.*, 2004). In both cereals, long days induce the expression of the photoperiod gene *PPD1*, a *PSEUDO-RESPONSE REGULATOR* (*PRR*) gene that controls the expression of *FT1* (Turner *et al.*, 2005; Kitagawa *et al.*, 2012; Shaw *et al.*, 2013). Taken together, the molecular networks that control *FT* expression are conserved between plant species; however, differences may occur depending on the plant's growth habit (Fig. 1). These subtle but important differences ensure that *FT* expression and function are tightly regulated to integrate environmental signals. This, in turn, safeguards proper developmental timing or flowering induction tailored to the surroundings of the plant.

FT is a mobile signal that moves from the leaves to the shoot apical meristem

FT is a member of the *PHOSPHATIDYLETHANOLAMINE BINDING PROTEIN* (*PEBP*) family, whose members are known to be regulators of phase transitioning, such as flowering initiation (Khosa *et al.*, 2021). The identification of FT protein as the florigen (Corbesier *et al.*, 2007) happened relatively recently, considering that the idea of a mobile flowering-inducing signal was first postulated in the 1930s (Knott, 1934; Chailakhyan, 1936; reviewed in Zeevaart, 2008). The mobility of FT from leaf to the SAM forms an integral part of its function. Under inductive conditions, *FT* is expressed in the leaf phloem companion cells (Takada and Goto, 2003; Chen *et al.*, 2018). FT protein is then loaded into the sieve elements (Mathieu *et al.*, 2007) and translocated via the bulk flow to the SAM, where it induces flowering (Corbesier *et al.*, 2007). The long-range movement of FT is not restricted to FT protein, as *FT* mRNA is also capable of moving through the plant via long-distance transport (Corbesier *et al.*, 2007; Li *et al.*, 2009, 2011; Lu *et al.*, 2012), although its functional relevance is still largely uncharacterized (reviewed in Jackson and Hong, 2012; Yu *et al.*, 2022). FT's mobility depends on both long-distance transport via the phloem and short-distance cell-to-cell transport at the site of synthesis and action, that is, at the leaf phloem companion cells and within the SAM, respectively. Aside from FT, other PEBP members are also capable of moving through the plant. In the model plant Arabidopsis, for example, TERMINAL FLOWER 1 (TFL1) moves within the meristem to control meristem development (Conti and Bradley, 2007; Goretti *et al.*, 2020) and in the developing seeds, where it regulates seed size (B. Zhang *et al.*, 2020). These observations suggest that cell-to-cell transport is an integral part of PEBP function.

There are two main described mechanisms that are involved in FT transport. One mechanism is via FT interaction with the multiple C2 domain and transmembrane region protein (MCTP) proteins. In Arabidopsis, three *MCTP* transporters of FT have been identified: *FT-INTERACTING PROTEIN 1* (*FTIP1*) (Liu *et al.*, 2012), *QUIRKY* (*QKY*) (Liu *et al.*, 2019), and *MCTP6* (Liu *et al.*, 2018). Plants lacking the function of any of these MCTPs exhibit a late flowering phenotype, consistent with the proposed lack of FT transport (Liu *et al.*, 2012, 2018, 2019). A second mechanism through which FT transport is mediated is via the direct interaction of FT with the cellular membranes. Interestingly, transport of FT from the companion cells to the sieve elements is a temperature-regulated process (Liu *et al.*, 2020; Susila *et al.*, 2021). At lower temperatures, when *FT* expression is reduced (Blázquez *et al.*, 2003), FT protein is sequestered at the level of the membranes via interaction with the phospholipid phosphatidylglycerol (Susila *et al.*, 2021). Since the association of FT with the cellular membranes is temperature dependent (Susila *et al.*, 2021), this environmental factor can, in addition to regulating *FT* expression,

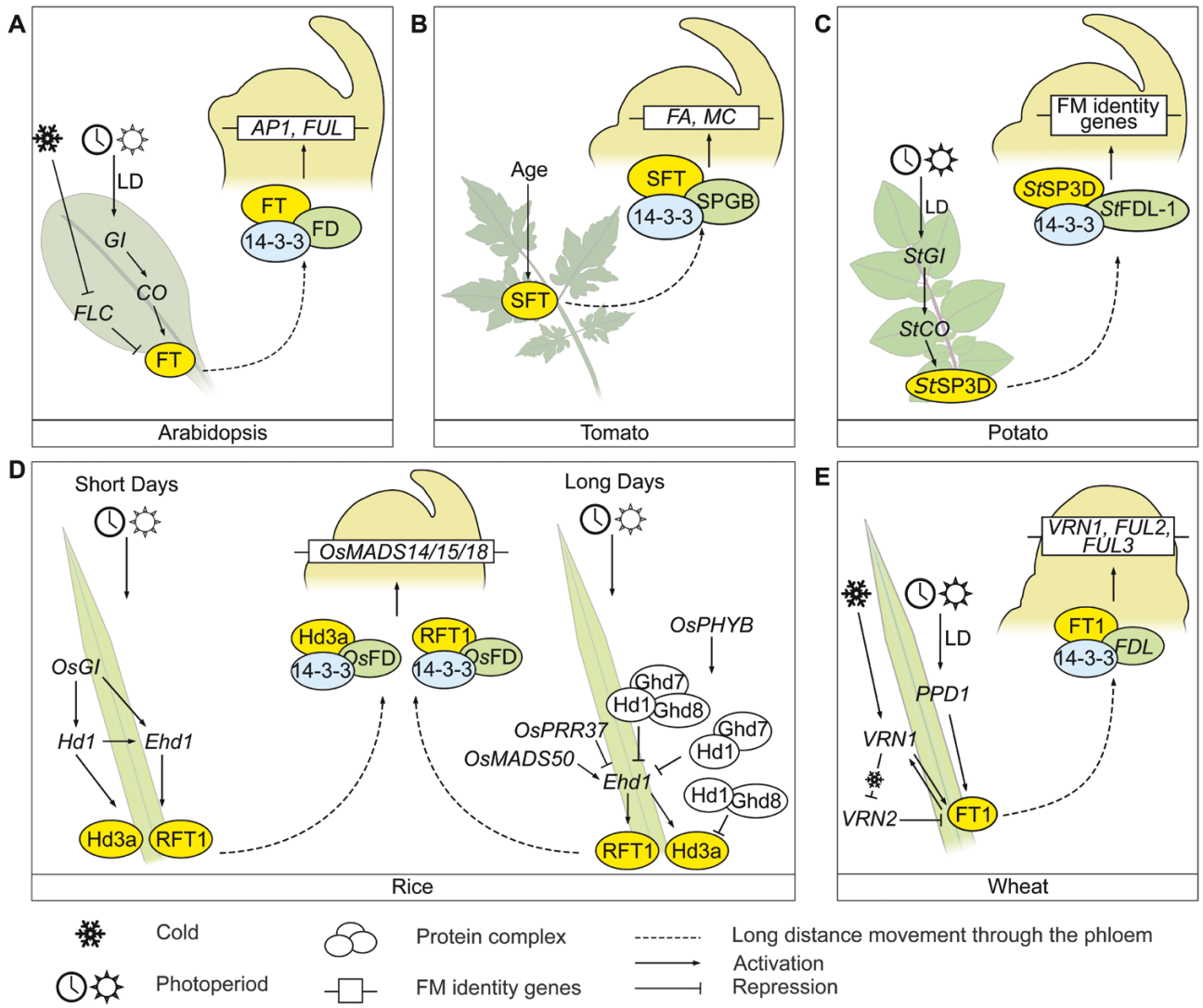

Fig. 1. The final trigger that promotes floral transition is conveyed by FT and its orthologues in Arabidopsis (A), tomato (B), potato (C), rice (D), and wheat (E). Upon perception of different environmental (e.g. cold and/or photoperiod) and internal (e.g. age) stimuli, FT is produced in the leaves and travels to the shoot apical meristem, where it forms a complex with FD and 14-3-3 proteins to regulate the transcription of floral meristem identity genes such as *AP1/FUL MADS-box* genes. *AP1*, *APETALA 1*; *CO*, *CONSTANS*; *Ehd1*, *Early heading date 1*; *FA*, *FALSIFLORA*; *FDL*, *FD-like*; *FLC*, *FLOWERING LOCUS C*; *FD*, *FLOWERING LOCUS D*; *FT*, *FLOWERING LOCUS T*; *FUL*, *FRUITFULL*; *GI*, *GIGANTEA*; *Ghd7*, *Grain number, plant height and heading date 7*; *Hd1*, *Heading date 1*; *Hd3a*, *Heading date 3a*; LD, long days; *MC*, *MACROCALYX*; *OsPHYB*, *RICE PHYTOCHROME B*; *PPD1*, *PHOTOPERIOD 1*; *OsPRR37*, *PSEUDO-RESPONSE REGULATOR 37*; *RFT1*, *RICE FLOWERING LOCUS T-1*; *SPGB*, *SELF-PRUNING G-BOX*; *SFT*, *SINGLE FLOWER TRUSS*; *VRN1*, *VERNALIZATION 1*; *VRN2*, *VERNALIZATION 2*.

also impact on FT transport directly. Together, this constitutes another layer of control over the flowering time transition. Within the phloem, FT is actively transported (Endo *et al.*, 2018) by interacting with the heavy metal binding protein SODIUM POTASSIUM ROOT DEFECTIVE 1 (NaKR1) (Zhu *et al.*, 2016). The unloading of FT from the phloem sap to the provascular tissue underneath the SAM is still uncharacterized, although some key residues in the FT protein have been suggested to be involved in this process (Endo *et al.*, 2018). The bulk flow within the phloem is non-selective and, as such, the gating mechanism that controls FT mobility occurs at its on- and off-loading from the phloem and within cell-to-cell transport through plasmodesmata. Therefore, understanding the mechanisms of this transport are of key interest to gain deeper insights into the control of FT and, thereby, flowering induction.

The florigen activation complex

Once imported into the cells of the SAM, FT acts as a transcriptional cofactor. First, it contacts 14-3-3 proteins in the

cytosol, forming a complex, which is then transported into the nucleus (Taoka *et al.*, 2011; Li *et al.*, 2015). Here, FT interacts with the A-class bZIP transcription factor FLOWERING LOCUS D (FD), with the 14-3-3 proteins bridging and reinforcing this interaction. Collectively, the formed heterohexameric complex is called the florigen activation complex (FAC) (Taoka *et al.*, 2011). Within the FAC, the transcription factor FD binds to the DNA to induce the expression of floral identity genes, including *APETALA1/FRUITFULL* (*AP1/FUL*) MADS-box genes (Abe *et al.*, 2005; Wigge *et al.*, 2005; Komiya *et al.*, 2008; Li and Dubcovsky, 2008; Digel *et al.*, 2015; Gao *et al.*, 2018; K. Li *et al.*, 2021; Jiang *et al.*, 2022). The interaction between FT-like proteins and FD is highly conserved across angiosperms (Pnueli *et al.*, 2001; Li *et al.*, 2015; Leeggangers *et al.*, 2018; Cerise *et al.*, 2020; Moraes *et al.*, 2022).

Taken together, FT is a key integration factor that moves, after its production in the leaf, to the SAM, where it forms an FAC to induce flowering. As such, FT is a mobile protein that connects signals perceived in the leaves to induce a transition in the meristem.

Balancing florigens with anti-florigens to control the timing of development

Three phylogenetic clades can be identified in the *PEBP* gene family: *FT-like*, *TFL1-like*, and *MOTHER OF FT AND TFL1 (MFT)-like*. Interestingly, besides *FT*, other members of the family are involved in the regulation of flowering time. In Arabidopsis, the *FT-like* gene *TWIN SISTER OF FT* (*TSF*) is partially redundant with *FT*, and promotes flowering under non-inductive conditions (Yamaguchi *et al.*, 2005). *TFL1*, the founding member of the *TFL1-like* clade, has an opposite effect on flowering time, maintaining the SAM in a vegetative state instead of initiating floral transition (Conti and Bradley, 2007). In contrast to FT, only short-range movement has been reported for TFL1, which is constitutively expressed in the central region of the SAM and translocated to the outer epidermal layer L1 (Conti and Bradley, 2007; Goretti *et al.*, 2020). Nevertheless, the creation of a transcriptional complex with FD-like and 14-3-3 proteins is a shared mechanism between FT/FT-like and TFL1/TFL1-like proteins (Kaneko-Suzuki *et al.*, 2018). Most importantly, the ability to interact with common partners lies at the core of the reported antagonism between the two clades (Kaneko-Suzuki *et al.*, 2018; Collani *et al.*, 2019; Zhu *et al.*, 2020). Within the FAC, TFL1 competes with FT for binding to FD, in both the active phosphorylated state and the inactive unphosphorylated state, and thereby prevents flowering induction (Taoka *et al.*, 2011; Kawamoto *et al.*, 2015; Collani *et al.*, 2019). Moreover, TFL1 in complex with FD acts as a direct transcriptional repressor of floral meristem identity genes or flowering time genes, some of which are targets of FT, for example, the pioneer transcription factor *LEAFY* (*LFY*) (Hanano and Goto, 2011; Zhu *et al.*, 2020). The model of competition between FT and TFL for FD interaction is conserved in several plant species, including dicots and monocots (Kaneko-Suzuki *et al.*, 2018). In rice, for example, the antiflorigen RICE CENTRORADIALIS 3 (RCN3) is able to form a florigen repression complex (FRC) with the 14-3-3 protein Gf14b and the *FD* homologue OsFD1 (Kaneko-Suzuki *et al.*, 2018).

Although direct competition for FAC/FRC formation has been directly confirmed only in Arabidopsis and rice (Kaneko-Suzuki *et al.*, 2018; Collani *et al.*, 2019; Zhu *et al.*, 2020), it is known in other species that the balance between *FT-like* and *TFL1-like* genes plays a critical role in the regulation of phase transition and developmental processes. In tomato, the *FT-like* gene *SINGLE FLOWER TRUSS* (*SFT*) and the *TFL1-like* gene *SELF PRUNING* (*SP*) are known to have contrasting effects on the regulation of termination of sympodial growth (Pnueli *et al.*, 1998; Lifschitz and Eshed, 2006; Lifschitz *et al.*, 2006) (Fig. 2E). The relative abundance (dosage) of SFT, SP, and other PEBPs is critical in the regulation of both flowering time and overall shoot architecture (Lifschitz and Eshed, 2006; Krieger *et al.*, 2010; Park *et al.*, 2012; Jiang *et al.*, 2013; Cao *et al.*, 2016; Soyk *et al.*, 2017; Gaarslev *et al.*, 2021). Together, *SFT* and *SP* control the rate at which meristems develop and acquire a new identity (Park *et al.*, 2012). Such a role for the PEBPs has also been observed in other crops. For example, the barley *TFL1-like* gene *CENTRORADIALIS* (*HvCEN*) influences the number of grains per spike by regulating the speed of inflorescence development (Bi *et al.*, 2019). In particular, *HvCEN* can promote both spikelet initiation, by interacting with the *FT-like* gene *HvFT3*, and subsequent floret development, by interacting with *HvFT1* (Bi *et al.*, 2019). Overall, it seems that PEBPs affect phase transitions and associated architectural changes by finely tuning the timing of each phase via a dosage-dependent mechanism.

Diversification of the PEBP family members and their impact on plant architecture

In the *Poaceae* (Chardon and Damerval, 2005; Dong *et al.*, 2020; Bennett and Dixon, 2021) and *Solanaceae* (Zhang *et al.*, 2022; Y. Sun *et al.*, 2023), there has been a notable expansion of the *PEBP* gene family, both via whole-genome duplication and through segmental or tandem duplications, coupled with neo- or subfunctionalization of the different members (Bennett and Dixon, 2021). A nice example is provided by the rice *FT-like* genes *Hd3a* and *RFT1*, which arose from a recent tandem duplication followed by subfunctionalization (Chardon and Damerval, 2005). *Hd3a* is the main florigen under SD conditions, whereas under LD conditions the role is fulfilled by *RFT1* (Tamaki *et al.*, 2007; Komiya *et al.*, 2008, 2009). Although there is still little known about the exact functions of all the different homologues that are derived from the duplication events and

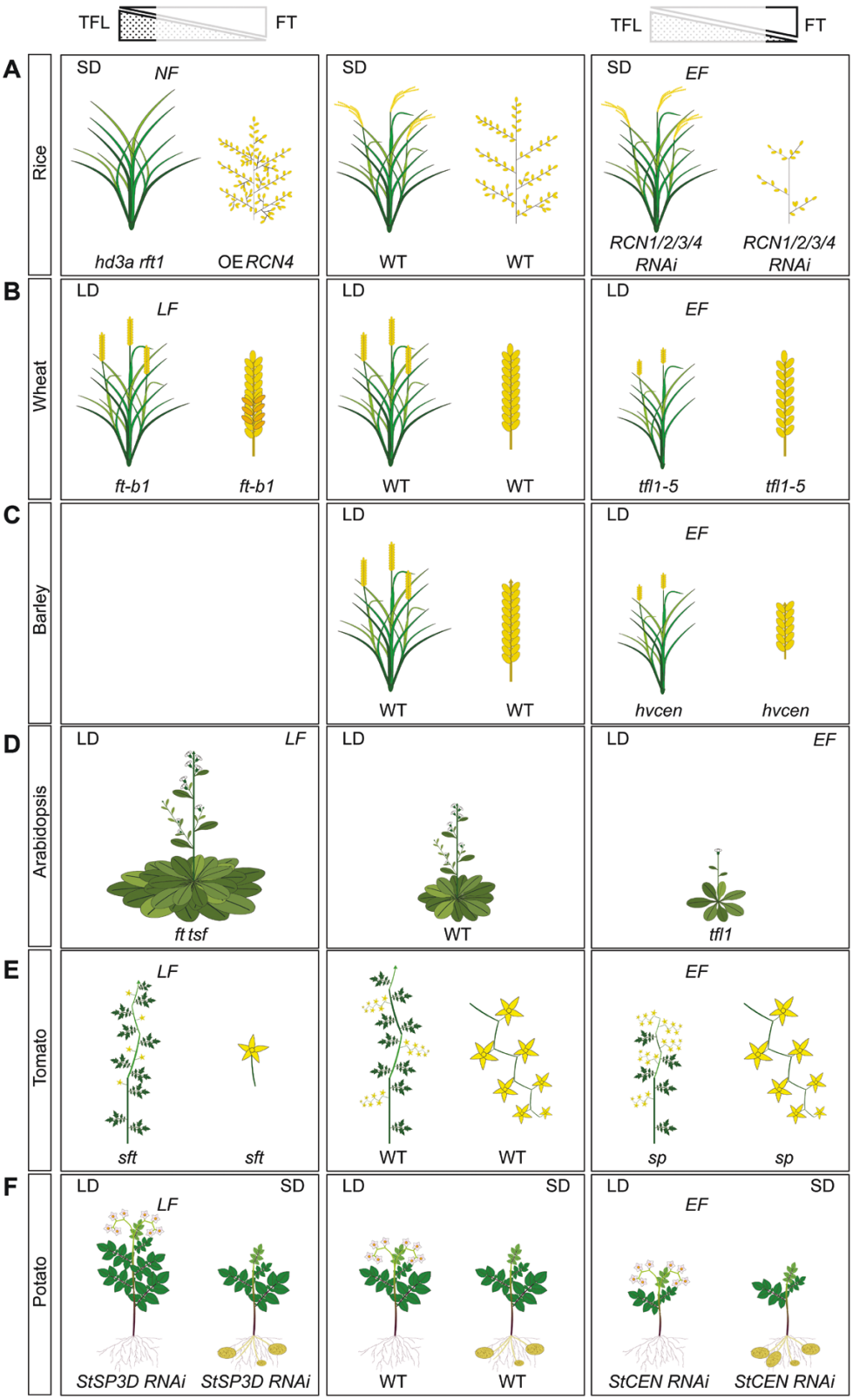

Fig. 2. Effect of FT–TFL balance on flowering time, plant architecture, and inflorescence architecture. The balance between FT and TFL has an effect on the plant phenotype; an overview of the phenotype of plants with high TFL or low FT (left column), and high FT or low TFL (right column), is shown. The phenotype of the wild type (WT) is represented in the central column. (A) In rice, *hd3a rft1* mutants are unable to flower under inductive and non-inductive

conditions (Giaume *et al.*, 2023). Panicles of plants overexpressing *RCN4* are shorter than those of the WT and highly branched (Zhu *et al.*, 2020). The quadruple knockdown of *RCN1/2/3/4* presents a mild early-flowering phenotype, coupled with a strong panicle phenotype, with a reduced number of branches and grains (C. Liu *et al.*, 2013). (B) Wheat *ft-b1* mutants present a strong late-flowering phenotype and paired spikelets (Boden *et al.*, 2015). *tfl1-5* plants flower earlier compared with the WT, and present a lower number of tillers. The number of grains per spike is also reduced (J. Sun *et al.*, 2023). (C) In barley, *hvcen* mutants are early flowering and have a lower number of tillers; plant height and spike length is reduced (Bi *et al.*, 2019). No data are available on the phenotype of *hvft1* knockout mutants. (D) When both *FT* and *TSF* are mutated (*ft tsf*), Arabidopsis plants flower later than the WT. Knocking out *TFL1* results in an early-flowering plant with an inflorescence that terminates in a terminal flower (Conti and Bradley, 2007), hence the name. (E) Plant architecture and inflorescence architecture are modified in the tomato *sft* mutant (Molinero-Rosales *et al.*, 2004). After the transition of the apex from vegetative to reproductive, also in this case earlier than in the WT, the newly formed transition meristem retrogresses to a vegetative state after forming one or two single flowers. Sympodial units are then formed from the repetitive cycles of floral transition and return to a vegetative state. Inflorescence architecture is not altered in *sp* mutants, whereas changes in the sympodial growth patterns are observed. The main apex transitions earlier and the growth terminates after three sympodial units (Pnueli *et al.*, 1998). (F) In potato, knockdown of the *FT-like* gene *StSP3D* causes a late-flowering phenotype under long days, but no effect on tuber formation under short days (Navarro *et al.*, 2011). A reduced level of *StCEN* expression leads to an early-flowering phenotype under long days and increased tuberization under short days (X. Zhang *et al.*, 2020). *CEN*, *CENTRORADIALIS*; EF, early flowering; *FT*, *FLOWERING LOCUS T*; *Hd3a*, *Heading date 3a*; LF, late flowering; LD, long-day conditions; NF, not flowering; OE, overexpressing; *RCN*, *RICE CENTRORADIALIS*; RNAi, RNA interference; *RFT1*, *RICE FLOWERING LOCUS T-1*; SD, short-day conditions; *SP*, *SELF PRUNING*; *SFT*, *SINGLE FLOWER TRUSS*; *TFL*, *TERMINAL FLOWER*; *TFL1*, *TERMINAL FLOWER* 1; *TSF*, *TWIN SISTER OF FT*.

are still present in the various plant genomes, it is likely that they are important for the fine-tuning of both flowering time and plant architecture.

There is an increasing amount of evidence that PEBPs are more than just floral integrators. In recent years, PEBP family members have been linked with different biological processes, such as the regulation of plant height, tiller number, and inflorescence architecture (Zhang *et al.*, 2005; Conti and Bradley, 2007; Bi *et al.*, 2019; Shaw *et al.*, 2019; Zhu *et al.*, 2021; Giaume *et al.*, 2023), storage organ formation (Navarro *et al.*, 2011; X. Zhang *et al.*, 2020; Jing *et al.*, 2023; recently reviewed in Khosa *et al.*, 2021; Susila and Purwestri, 2023), and seed germination and dormancy (Xi *et al.*, 2010; Nakamura *et al.*, 2011; S. Liu *et al.*, 2013) (Fig. 2). For example, *FT2* in barley and wheat, and its orthologue in rice, *OsFT-L1*, have only a minor role in the regulation of flowering time, and are mainly involved in the determination of inflorescence architecture (Shaw *et al.*, 2019; Gauley and Boden, 2021; Giaume *et al.*, 2023). Mutants in wheat *FT2* show a slight delay in heading date, coupled with an increase in spikelet number, suggesting that progression to the terminal spikelet stage is slowed in *ft2* mutants (Shaw *et al.*, 2019; Gauley and Boden, 2021). Similarly, *RCN4* in rice is also involved in the regulation of panicle architecture (Zhu *et al.*, 2021). Tiller and spikelet numbers are reduced in knockout lines for the *TFL1* orthologues in barley (*hvcen*; Bi *et al.*, 2019) and wheat (*tatfl1-5*; J. Sun *et al.*, 2023).

In tuberous crops, PEBPs are involved in the regulation of both flowering and tuber formation. In potato, tuberization is initiated under SD conditions, when the expression of the tuberigen *SELF-PRUNING 6A* (*StSP6A*) is induced in the leaves (Navarro *et al.*, 2011). In a similar fashion to that reported for florigens, StSP6A is transported from the leaves. Ultimately, it promotes *StMADS1* and *StMADS13* expression in the stolons, resulting in tuberization (Navarro *et al.*, 2011; Gao *et al.*, 2018). Transcriptional regulation by StSP6A is achieved via the creation of a tuberigen activation complex (TAC) with FD-like proteins and 14-3-3 proteins (Teo *et al.*, 2017). Interestingly, StSP6A affects tuber formation and floral bud development in opposite ways (Plantenga *et al.*, 2019). The *TFL1/CEN* orthologue StCEN inhibits tuber initiation and development by directly competing with StSP6A for the formation of a tuberigen complex (X. Zhang *et al.*, 2020), analogous to the competition reported for FT-like and TFL1-like proteins in the regulation of floral transition in rice and Arabidopsis (Kaneko-Suzuki *et al.*, 2018; Collani *et al.*, 2019; Zhu *et al.*, 2020). It has recently been shown that the florigens StSP3D and FT-like 1 (*StFTL1*) can induce tuber formation in a photoperiod-dependent manner, promoting *StMADS1* and *StMADS13* expression and subsequently reinforcing *StSP6A* expression in the developing tubers (Jing *et al.*, 2023). Taken together, these findings indicate that PEBP proteins not only modulate flowering time but also have an impact on storage organ formation and plant architecture.

Regulation of flowering time by members of the *TCP* gene family

TCP genes belong to a plant-specific family of transcription factors named after the founding members *TEOSINTE BRANCHED 1* (*TB1*) in maize (*Zea mays*), *CYCLOIDEA* (*CYC*) in snapdragon (*Antirrhinum majus*), and *PROLIFERATING CELL NUCLEAR ANTIGEN FACTORS 1* and *2* (*PCF1* and *PCF2*) in rice (Cubas *et al.*, 1999). *ZmTB1* regulates branching by inhibiting axillary bud outgrowth, and as such has been critical for maize domestication from the ancestor teosinte (Doebley *et al.*, 1995, 1997). *AmCYC* is implicated in the determination of the dorsoventral asymmetry characteristics of snapdragon flowers (Luo *et al.*, 1996). OsPCF1 and OsPCF2 homo- and heterodimerize to bind to *cis*-elements in the promoter of the cell cycle regulator *PROLIFERATING CELL NUCLEAR ANTIGEN* (*PCNA*), driving its expression in the meristem (Kosugi and Ohashi, 1997). Such a diversity in the functions of the founding members of the TCP family mirrors the functional diversity that can be found throughout the entire family. Based on phylogenetic

studies, the TCPs can be classified into two groups, class I and class II (Cubas *et al.*, 1999). Members in class II can be additionally grouped into two distinct clades, namely the *CINCINNATA* (*CIN*) clade and the *CYC/TB1* clade (Nath *et al.*, 2003; Howarth and Donoghue, 2006). TCP proteins are implicated in the regulation of several biological processes, mainly by tuning cell proliferation and growth. Several reviews have been published on this topic over the years (Rath *et al.*, 2022; Zhou *et al.*, 2022; Viola and Gonzalez, 2023; Viola *et al.*, 2023). Initially, the ability to directly control the transcription of cell-cycle regulators (Manassero *et al.*, 2013; Nicolas and Cubas, 2016a) was thought to be shared among all members of the TCP family (Cubas *et al.*, 1999). However, it seems more and more likely that TCPs act on plant growth and architecture, conveyed via both direct and indirect regulation of cell-proliferation genes (Efroni *et al.*, 2008; Danisman *et al.*, 2012). In addition, TCPs are implicated in different hormonal signalling pathways (Nicolas and Cubas, 2016a). TCPs have also been shown to be involved in developmental processes such as flowering time, whole-plant and inflorescence architecture (Ramsay *et al.*, 2011; Bai *et al.*, 2012; S. Wang *et al.*, 2015; Nicolas and Cubas, 2016b; Dixon *et al.*, 2018; de Souza Moraes *et al.*, 2022), and fertility (Jin *et al.*, 2011; Jiao *et al.*, 2018; Gladman *et al.*, 2019; de Souza Moraes *et al.*, 2022). TCP members are additionally engaged in drought tolerance (Ding *et al.*, 2019; Urano *et al.*, 2022; Gull *et al.*, 2023; Jiao *et al.*, 2023) and plant defence (Kim *et al.*, 2014; X. Wang *et al.*, 2015; Bao *et al.*, 2019; Wang *et al.*, 2019).

The interaction between PEBP proteins and TCP family members has been reported in multiple species and is thought to contribute to the regulation of flowering time and whole-plant or inflorescence architecture. A first example of such an interaction has been characterized in apple (*Malus domestica*), where MdTCP4a and MdTCP2a, respectively orthologues of the miR319-regulated class II CIN TCPs AtTCP4 and AtTCP2, have been identified as potential interactors of MdFT (Mimida *et al.*, 2011). The interaction between TCPs and PEBPs has been studied in detail in Arabidopsis. Here, the class II CYC-TB1 member BRANCHED 1 (BRC1), homologous to the founding member TB1, is able to interact with FT and TWIN SISTER OF FT (TSF) to control the flowering of axillary branches (Niwa *et al.*, 2013). The ability of FT to interact with TCPs is extended to several members of both class I and class II TCPs (Ho and Weigel, 2014). Moreover, the specificity reported for BRC1 binding of FT but not TFL1 seems to be shared by other class I and class II members, thereby suggesting that some of the key residues identified as markers for an FT or TFL1-like activity may be involved in the creation of such an interaction (Ho and Weigel, 2014). The interaction of BRC1 with FT and TSF might explain the early-flowering phenotype in *brc1* mutants (Niwa *et al.*, 2013), in which the florigens are not titrated by interaction with BRC1. This effect is not unique to Arabidopsis; for example, in rye (*Secale cereale*) ScTCP9 can interact with ScFT and potentially regulate flowering time by disturbing the formation of the FAC (Zhan *et al.*, 2023). Similarly, in *Brassica juncea*, the interaction between BjuBRC1-1 and BjuFT is suggested to be important for the negative regulation of flowering time (Feng *et al.*, 2022). In hybrid aspen (*Populus tremula* × *tremuloides*), the TB1 orthologue BRC1 is a key regulator of seasonal growth, being able to bind and sequester the FT-like protein FT2, thus promoting growth cessation under non-inductive conditions (Maurya *et al.*, 2020). In Arabidopsis, BRC1 interacts with both FD and FT (Niwa *et al.*, 2013; Ho and Weigel, 2014; Li *et al.*, 2019). Similarly, the class II CIN TCPs AtTCP5, AtTCP13, and AtTCP17 are able to interact at the protein level with FD, and can act by facilitating the binding of FD to target loci (Li *et al.*, 2019).

The above examples are focused on the interaction of TCPs with the FAC components FT and FD. However, TCPs are involved in the regulation of flowering time at different levels (recently reviewed in Viola and Gonzalez, 2023). In Arabidopsis, AtTCP20 and AtTCP22 can influence flowering time by directly regulating the expression of the clock component *CIRCADIAN CLOCK ASSOCIATED 1* (*CCA1*), in a LIGHT-REGULATED WDs (LWDs)-dependent mechanism (Wu *et al.*, 2016) or by forming photobodies with CRYPTOCHROME 2 (CRY2) upon blue light exposure (Mo *et al.*, 2022). In the same model organism, *CONSTANS* (*CO*) expression is under the control of miR319-regulated class II CIN TCPs (Kubota *et al.*, 2017; Liu *et al.*, 2017). In particular, AtTCP4 is able to promote *CO* expression in a *GIGANTEA* (*GI*)-dependent and -independent way, interacting with either GI (Kubota *et al.*, 2017) or the flowering regulators FLOWERING BHLH (FBHs) and PHYTOCHROME AND FLOWERING TIME 1 (PFT1) (Liu *et al.*, 2017). Downstream in this pathway, TCPs can regulate flowering by acting at the level of the flowering integrators *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*) and *FT* (Balsemão-Pires *et al.*, 2013; Lucero *et al.*, 2017; X. Li *et al.*, 2021; Camoirano *et al.*, 2023). Conversely to what has been reported in Arabidopsis, the *TCP4* orthologue in tomato, *LANCEOLATE* (*LA*), has a negative effect on flowering via direct or indirect repression of the *FT-like* gene *SFT* and the *MADS-box* gene *APETALA1/MACROCALYX* (*AP1/MC*) (Silva *et al.*, 2019). This exemplifies that subtle yet important mechanistic differences may occur between species. Taken together, TCP proteins modulate flowering time through interacting with components of the FAC, but also through direct control of key flowering time-related genes.

TCP and PEBP interaction and plant architecture: a spotlight on TB1 orthologues

One of the most well-known members of the *TCP* transcription factor family is *TB1* (Doebley *et al.*, 1995). Originally, *TB1* was identified as the key domestication-related gene in

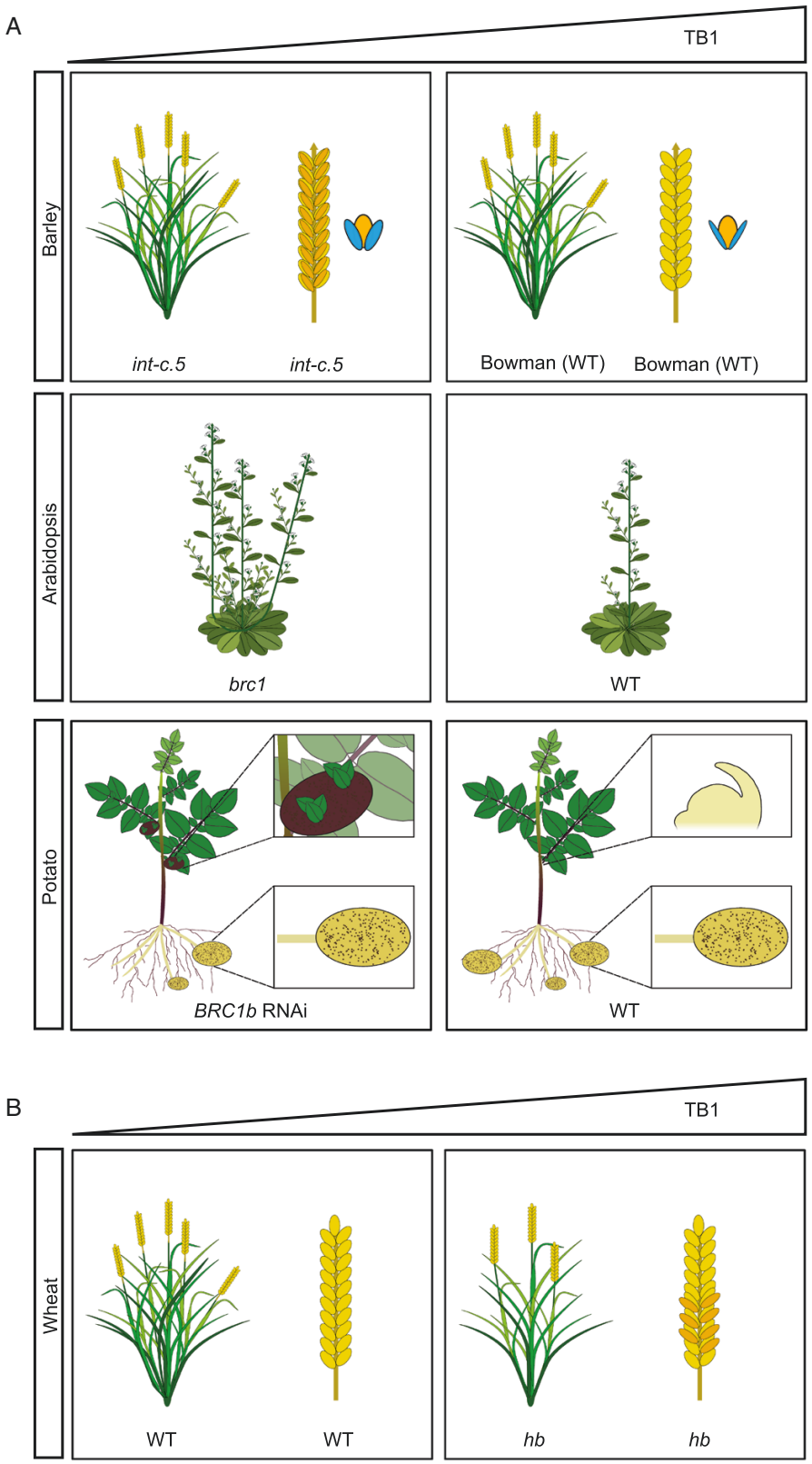

Fig. 3. Low or high *TB1* dosage strongly affects plant architecture. (A) In barley, *int-c.5* mutants carry a frameshift mutation in *HvTB1* (Ramsay *et al.*, 2011). *int-c.5* mutants in a Bowman background present a high tillering phenotype during early development (Ramsay *et al.*, 2011; Liller *et al.*, 2015). Spikes of the *int-c.5* mutant have an intermediate phenotype, with partial development of the lateral spikelets. In Arabidopsis, the *brc1* mutant has a similar branched shoot phenotype, caused by axillary bud outgrowth (Aguilar-Martínez *et al.*, 2007). Potato *BRC1b* RNAi plants also show outgrowth

of axillary buds, in this case accompanied by aerial tuber formation (Nicolas *et al.*, 2022). (B) The wheat *hb* mutant has been selected from a MAGIC population, following the paired spikelet phenotype in the spikes. This phenotype results from an increased dosage of *TB-D1* in the line due to tetrasomy of chromosome 4D. *hb* plants also present a lower tiller number compared with the wild-type (Dixon *et al.*, 2018). *BRC1*, *BRANCHED* 1; *hb*, *highly-branched*; *int-c*, *Intermedium-c*; *TB1*, *TEOSINTE BRANCHED* 1.

maize, where the insertion of a transposable element called *HOPSCOTCH* resulted in an increased dosage of *ZmTB1*. In turn, the increased *ZmTB1* level caused a complete suppression of axillary branching. Since its original discovery, orthologues of *TB1* have been identified as major players that control plant architecture and yield in various crops (Fig. 3), including rice, barley, and wheat (Doebley *et al.*, 1997; Takeda *et al.*, 2003; Ramsay *et al.*, 2011; Dixon *et al.*, 2018). The core function of these orthologues, as negative regulators of bud outgrowth, is conserved in angiosperms. In cereals, they are also known to modulate inflorescence architecture. Barley plants that carry a loss-of-function allele of the *TB1* orthologue *vulgare row-type spike (VRS) 5,* for example, exhibit increased development of lateral florets, and an increased tiller number early in development (Ramsay *et al.*, 2011; Liller *et al.*, 2015) (Fig. 3A, top panel). Recent comparative network analysis of *AtBRC1* and *ZmTB1* suggested that both genes control abscisic acid (ABA) hormone signalling. In the model plant Arabidopsis, BRC1 binds directly to the promoter of homeodomain leucine zipper (HD-ZIP) transcription factors. This results in the initiation of ABA signalling and the suppression of bud outgrowth (González-Grandío *et al.*, 2017; van Es *et al.*, 2024). The activation of HD-ZIP family members by TB1 is conserved in maize. Here, ZmTB1 targets the HD-ZIP transcription factor *ZmGRASSY TILLERS* (*ZmGT1*) in addition to ABA signalling components (Whipple *et al.*, 2011; Dong *et al.*, 2019). This suggests that this core regulatory control on shoot branching is evolutionarily ancient, predating the separation of monocots and dicots (van Es *et al.*, 2024).

Similarly, the interaction between homologues of FT and TB1 is highly conserved across the plant kingdom (Niwa *et al.*, 2013; Dixon *et al.*, 2018), and provides an initial and direct link between flowering time and genes that control plant architecture. This interaction, however, does not always have an impact on flowering time as is the case in BRC1–FT1 interaction. In wheat, for example, the *TB1* D-homeologue (TB-D1) interacts with FT1, preventing the formation of an FAC with 14-3-3 proteins and other FD-like proteins (Dixon *et al.*, 2018). As a consequence, an increased dosage of TB-D1, as is observed in the *highly-branched* (*hb*) mutants, results in a slight delay of the early phases of inflorescence development. This ultimately leads to the production of paired spikelets (Fig. 3B), a phenotype also observed in *ft-b1* mutants (Boden *et al.*, 2015). Nonetheless, no effect on flowering time has been reported in wheat *hb* lines that have an increased dosage of *TB-D1* (Dixon *et al.*, 2018). In potato, tuberization is controlled by the *FT-like StSP6A* gene, and the StSP6A protein interacts directly with the TCP StBRC1b (Nicolas *et al.*, 2022). *StSP6A* is expressed under SD conditions (Susila and Purwestri, 2023), whereas under LD conditions, *StSP6A* is suppressed by a *CONSTANS-LIKE* transcription factor (*StCOL1*), which acts through the activation of *StSP5G*, another PEBP family member (Abelenda *et al.*, 2016). In the absence of StSP5G, *StSP6A* is expressed in the leaf tissue and transported to the stolon, where it forms an activation complex that induces tuberization below ground. Tuberization above ground is prevented as StSP6A protein is bound, and antagonized, by StBRC1b (Nicolas *et al.*, 2022). In the absence of a functional *StBRC1b*, the axillary buds in the aerial parts of the plant become strong sinks, competing for resources with the tubers below ground (Nicolas *et al.*, 2022). This leads to an accumulation of photoassimilates in the aerial buds that normally would have been transported to the tubers (Nicolas *et al.*, 2022). As a consequence, ectopic aerial tubers are formed in *brc1b* mutants, at the cost of underground tuberization. This mechanism exemplifies that TCPs, in this case *StBRC1b*, can act as gatekeepers of the source/sink balance, potentially in an interplay with PEBP family members (Susila and Purwestri, 2023). In conclusion, *TB1-like* TCP transcription factors form a conserved central hub that controls plant architecture and development, potentially through modulation of the source/sink balance and interaction with PEBP family members.

Conclusions and perspectives

Flowering time is tightly regulated by the interplay of FT and TFL1, which form a complex with the transcription factor FD. Recent research indicates that FT/TFL-like proteins also interact with TCP transcription factors, which are key regulators of plant architecture. Although the genetic and molecular interactions behind the interplay between PEBPs and TCPs seem to be conserved in crops, the roles of most of the members of the expanded gene families are still unknown. Similarly, a more in-depth knowledge of how different members of the same family interact with each other both genetically and physically is required. Additionally, little is known about the importance of the relative dosage among different orthologues, and how this impacts on the regulation of plant architecture and life cycle and, as a consequence, yield. With regard to this last point, a shift toward quantitative assays is required in order to better evaluate the possible competition that can occur and regulate the formation of the various complexes.

To conclude, in this review we have highlighted the intertwined role of PEBPs and TCPs in the regulation of flowering time and plant architecture. Both traits are critical in

determining the final yield, and it is therefore important to understand how this interplay takes place in crops.

Acknowledgements

We gratefully thank both anonymous reviewers for their excellent suggestions to improve our manuscript.

Author contributions

PEC generated the figures wrote the manuscript and conceived the review; SWvE and TW contributed to the section on the regulation of flowering time by TCPs; RGHI and GWvE corrected the manuscript, provided feedback and conceived the review. All authors provided feedback and approved the final version.

Conflict of interest

The authors declare no competing or financial interests.

Funding

This work was financially supported by a NWO-VIDI grant to GWvE (project number 18366), a NWO JSTP grant (no. 833.13.008), and a NWO-VICI grant to RGHI (project number 16129).

References

Abe M, Kobayashi Y, Yamamoto S, Daimon Y, Yamaguchi A, Ikeda Y, Ichinoki H, Notaguchi M, Goto K, Araki T. 2005. FD, a bZIP protein mediating signals from the floral pathway integrator FT at the shoot apex. Science **309**, 1052–1056.

Abelenda JA, Cruz-Oró E, Franco-Zorrilla JM, Prat S. 2016. Potato StCONSTANS-like1 suppresses storage organ formation by directly activating the FT-like *StSP5G* repressor. Current Biology **26**, 872–881.

Aguilar-Martínez JA, Poza-Carrión C, Cubas P. 2007. *Arabidopsis BRANCHED1* acts as an integrator of branching signals within axillary buds. The Plant Cell **19**, 458–472.

Bai F, Reinheimer R, Durantini D, Kellogg EA, Schmidt RJ. 2012. TCP transcription factor, BRANCH ANGLE DEFECTIVE 1 (BAD1), is required for normal tassel branch angle formation in maize. Proceedings of the National Academy of Sciences, USA **109**, 12225–12230.

Bai Y, Lindhout P. 2007. Domestication and breeding of tomatoes: what have we gained and what can we gain in the future? Annals of Botany **100**, 1085–1094.

Balsemão-Pires E, Andrade LR, Sachetto-Martins G. 2013. Functional study of TCP23 in *Arabidopsis thaliana* during plant development. Plant Physiology and Biochemistry **67**, 120–125.

Bao S, Zhang Z, Lian Q, Sun Q, Zhang R. 2019. Evolution and expression of genes encoding TCP transcription factors in *Solanum tuberosum* reveal the involvement of *StTCP23* in plant defence. BMC Genetics **20**, 91.

Bennett T, Dixon LE. 2021. Asymmetric expansions of FT and TFL1 lineages characterize differential evolution of the EuPEBP family in the major angiosperm lineages. BMC Biology **19**, 1–17.

Bi X, van Esse W, Mulki MA, Kirschner G, Zhong J, Simon R, von Korff M. 2019. CENTRORADIALIS interacts with *FLOWERING LOCUS T*-like genes to control floret development and grain number. Plant Physiology **180**, 1013–1030.

Blázquez MA, Ahn JH, Weigel D. 2003. A thermosensory pathway controlling flowering time in *Arabidopsis thaliana*. Nature Genetics **33**, 168–171.

Boden SA, Cavanagh C, Cullis BR, Ramm K, Greenwood J, Jean Finnegan E, Trevaskis B, Swain SM. 2015. *Ppd-1* is a key regulator of inflorescence architecture and paired spikelet development in wheat. Nature Plants **1**, 14016.

Bommert P, Satoh-Nagasawa N, Jackson D, Hirano HY. 2005. Genetics and evolution of inflorescence and flower development in grasses. Plant and Cell Physiology **46**, 69–78.

Bommert P, Whipple C. 2018. Grass inflorescence architecture and meristem determinacy. Seminars in Cell and Developmental Biology **79**, 37–47.

Cai M, Chen S, Wu M, *et al*. 2019. Early heading 7 interacts with DTH8, and regulates flowering time in rice. Plant Cell Reports **38**, 521–532.

Camoirano A, Alem AL, Gonzalez DH, Viola IL. 2023. The N-terminal region located upstream of the TCP domain is responsible for the antagonistic action of the *Arabidopsis thaliana* TCP8 and TCP23 transcription factors on flowering time. Plant Science **328**, 111571.

Cao K, Cui L, Zhou X, Ye L, Zou Z, Deng S. 2016. Four tomato FLOWERING LOCUS T-Like proteins act antagonistically to regulate floral initiation. Frontiers in Plant Science **6**, 1213.

Cerise M, Giaume F, Galli M, *et al*. 2020. OsFD4 promotes the rice floral transition via florigen activation complex formation in the shoot apical meristem. New Phytologist **229**, 429–443.

Chailakhyan MKH. 1936. On the hormonal theory of plant development. Comptes Rendus (Doklady) de l'Académie des Sciences de l'URSS **12**, 443–447.

Chardon F, Damerval C. 2005. Phylogenomic analysis of the PEBP gene family in cereals. Journal of Molecular Evolution **61**, 579–590.

Chen Q, Payyavula RS, Chen L, Zhang J, Zhang C, Turgeon R. 2018. *FLOWERING LOCUS T* mRNA is synthesized in specialized companion cells in *Arabidopsis* and Maryland Mammoth tobacco leaf veins. Proceedings of the National Academy of Sciences, USA **115**, 2830–2835.

Collani S, Neumann M, Yant L, Schmid M. 2019. FT modulates genome-wide DNA-binding of the bZIP transcription factor FD. Plant Physiology **180**, 367–380.

Conti L, Bradley D. 2007. TERMINAL FLOWER1 is a mobile signal controlling *Arabidopsis* architecture. The Plant Cell **19**, 767–778.

Corbesier L, Vincent C, Jang S, *et al*. 2007. FT protein movement contributes to long-distance signaling in floral induction of *Arabidopsis*. Science **316**, 1030–1033.

Cubas P, Lauter N, Doebley J, Coen E. 1999. The TCP domain: a motif found in proteins regulating plant growth and development. The Plant Journal **18**, 215–222.

Danisman S, van der Wal F, Dhondt S, *et al*. 2012. Arabidopsis Class I and Class II TCP transcription factors regulate jasmonic acid metabolism and leaf development antagonistically. Plant Physiology **159**, 1511–1523.

Deng W, Casao MC, Wang P, Sato K, Hayes PM, Finnegan EJ, Trevaskis B. 2015. Direct links between the vernalization response and other key traits of cereal crops. Nature Communications **6**, 5882.

de Souza Moraes T, van Es SW, Hernández-Pinzón I, *et al*. 2022. The TCP transcription factor HvTB2 heterodimerizes with VRS5 and controls spike architecture in barley. Plant Reproduction **35**, 205–220.

Digel B, Pankin A, von Korff M. 2015. Global transcriptome profiling of developing leaf and shoot apices reveals distinct genetic and environmental control of floral transition and inflorescence development in barley. The Plant Cell **27**, 2318–2334.

Ding S, Cai Z, Du H, Wang H. 2019. Genome-wide analysis of TCP family genes in *Zea mays* L. Identified a role for *ZmTCP42* in drought tolerance. International Journal of Molecular Sciences **20**, 2762.

Dixon LE, Greenwood JR, Bencivenga S, Zhang P, Cockram J, Mellers G, Ramm K, Cavanagh C, Swain SM, Boden SA. 2018. *TEOSINTE BRANCHED1* regulates inflorescence architecture and development in bread wheat (*Triticum aestivum*). The Plant Cell **30**, 563–581.

Dixon LE, van Esse W, Hirsz D, Willemsen V, McKim SM. 2022. Cereal architecture and its manipulation. Annual Plant Reviews Online. doi: 10.1002/9781119312994.apr0648

Doebley J, Stec A, Gustus C. 1995. *teosinte branched1* and the origin of maize: evidence for epistasis and the evolution of dominance. Genetics **141**, 333–346.

Doebley J, Stec A, Hubbard L. 1997. The evolution of apical dominance in maize. Nature **386**, 485–488.

Doi K, Izawa T, Fuse T, Yamanouchi U, Kubo T, Shimatani Z, Yano M, Yoshimura A. 2004. *Ehd1*, a B-type response regulator in rice, confers short-day promotion of flowering and controls *FT-like* gene expression independently of *Hd1*. Genes & Development **18**, 926–936.

Dong L, Lu Y, Liu S. 2020. Genome-wide member identification, phylogeny and expression analysis of PEBP gene family in wheat and its progenitors. PeerJ **8**, e10483.

Dong Z, Xiao Y, Govindarajulu R, Feil R, Siddoway ML, Nielsen T, Lunn JE, Hawkins J, Whipple C, Chuck G. 2019. The regulatory landscape of a core maize domestication module controlling bud dormancy and growth repression. Nature Communications **10**, 3810.

Du A, Tian W, Wei M, Yan W, He H, Zhou D, Huang X, Li S, Ouyang X. 2017. The DTH8-Hd1 module mediates day-length-dependent regulation of rice flowering. Molecular Plant **10**, 948–961.

Efroni I, Blum E, Goldshmidt A, Eshed Y. 2008. A protracted and dynamic maturation schedule underlies *Arabidopsis* leaf development. The Plant Cell **20**, 2293–2306.

Endo M, Yoshida M, Sasaki Y, Negishi K, Horikawa K, Daimon Y, Kurotani KI, Notaguchi M, Abe M, Araki T. 2018. Re-evaluation of florigen transport kinetics with separation of functions by mutations that uncouple flowering initiation and long-distance transport. Plant and Cell Physiology **59**, 1621–1629.

Feng J, Deng Q, Lu H, Wei D, Wang Z, Tang Q. 2022. *Brassica juncea BRC1*-1 induced by SD negatively regulates flowering by directly interacting with BjuFT and *BjuFUL* promoter. Frontiers in Plant Science **13**, 986811.

Fernández-Calleja M, Casas AM, Igartua E. 2021. Major flowering time genes of barley: allelic diversity, effects, and comparison with wheat. Theoretical and Applied Genetics **134**, 1867–1897.

Food and Agriculture Organization of the United Nations. 2023. FAOSTAT. https://www.fao.org/faostat/

Gaarslev N, Swinnen G, Soyk S. 2021. Meristem transitions and plant architecture—learning from domestication for crop breeding. Plant Physiology **187**, 1045–1056.

Gao H, Jin M, Zheng X-M, *et al*. 2014. *Days to heading 7*, a major quantitative locus determining photoperiod sensitivity and regional adaptation in rice. Proceedings of the National Academy of Sciences, USA **111**, 16337–16342.

Gao H, Wang Z, Li S, Hou M, Zhou Y, Zhao Y, Li G, Zhao H, Ma H. 2018. Genome-wide survey of potato MADS-box genes reveals that StMADS1 and StMADS13 are putative downstream targets of tuberigen StSP6A. BMC Genomics **19**, 726.

Gauley A, Boden SA. 2021. Stepwise increases in *FT1* expression regulate seasonal progression of flowering in wheat (*Triticum aestivum*). New Phytologist **229**, 1163–1176.

Giaume F, Bono GA, Martignago D, *et al*. 2023. Two florigens and a florigen-like protein form a triple regulatory module at the shoot apical meristem to promote reproductive transitions in rice. Nature Plants **9**, 525–534.

Gladman N, Jiao Y, Lee YK, *et al*. 2019. Fertility of pedicellate spikelets in sorghum is controlled by a jasmonic acid regulatory module. International Journal of Molecular Sciences **20**, 4951.

Gómez-Ariza J, Galbiati F, Goretti D, Brambilla V, Shrestha R, Pappolla A, Courtois B, Fornara F. 2015. Loss of floral repressor function adapts rice to higher latitudes in Europe. Journal of Experimental Botany **66**, 2027–2039.

González-Grandío E, Pajoro A, Franco-Zorrilla JM, Tarancón C, Immink RGH, Cubas P. 2017. Abscisic acid signaling is controlled by a *BRANCHED1/HD-ZIP I* cascade in *Arabidopsis* axillary buds. Proceedings of the National Academy of Sciences, USA **114**, E245–E254.

Goretti D, Martignago D, Landini M, *et al*. 2017. Transcriptional and post-transcriptional mechanisms limit Heading Date 1 (Hd1) function to adapt rice to high latitudes. PLoS Genetics **13**, e1006530.

Goretti D, Silvestre M, Collani S, Langenecker T, Méndez C, Madueño F, Schmid M. 2020. TERMINAL FLOWER1 functions as a mobile transcriptional cofactor in the shoot apical meristem. Plant Physiology **182**, 2081–2095.

Gull S, Uddin S, Hussain HA, Wang S, Bayar J, Liu J. 2023. Genome-wide analysis reveals the TCP-miR159-miR319 module is crucial for rice (*Oryza sativa* L.) growth and response to drought and salinity. Plant Stress **10**, 100215.

Hanano S, Goto K. 2011. *Arabidopsis* TERMINAL FLOWER1 is involved in the regulation of flowering time and inflorescence development through transcriptional repression. The Plant Cell **23**, 3172–3184.

Hayama R, Yokoi S, Tamaki S, Yano M, Shimamoto K. 2003. Adaptation of photoperiodic control pathways produces short-day flowering in rice. Nature **422**, 719–722.

Ho WWH, Weigel D. 2014. Structural features determining flower-promoting activity of *Arabidopsis* FLOWERING LOCUS T. The Plant Cell **26**, 552–564.

Howarth DG, Donoghue MJ. 2006. Phylogenetic analysis of the "ECE" (CYC/TB1) clade reveals duplications predating the core eudicots. Proceedings of the National Academy of Sciences, USA **103**, 9101–9106.

Huang X, Kurata N, Wei X, *et al*. 2012. A map of rice genome variation reveals the origin of cultivated rice. Nature **490**, 497–501.

Izawa T, Oikawa T, Sugiyama N, Tanisaka T, Yano M, Shimamoto K. 2002. Phytochrome mediates the external light signal to repress *FT* orthologs in photoperiodic flowering of rice. Genes and Development **16**, 2006–2020.

Jackson S, Hong Y. 2012. Systemic movement of FT mRNA and a possible role in floral induction. Frontiers in Plant Science **3**, 127.

Jackson SD. 1999. Multiple signaling pathways control tuber induction in potato. Plant Physiology **119**, 1–8.

Jiang K, Liberatore KL, Park SJ, Alvarez JP, Lippman ZB. 2013. Tomato yield heterosis is triggered by a dosage sensitivity of the florigen pathway that fine-tunes shoot architecture. PLoS Genetics **9**, e1004043.

Jiang X, Lubini G, Hernandes-Lopes J, Rijnsburger K, Veltkamp V, de Maagd RA, Angenent GC, Bemer M. 2022. FRUITFULL-like genes regulate flowering time and inflorescence architecture in tomato. The Plant Cell **34**, 1002–1019.

Jiao P, Liu T, Zhao C, Fei J, Guan S, Ma Y. 2023. *ZmTCP14*, a TCP transcription factor, modulates drought stress response in *Zea mays* L. Environmental and Experimental Botany **208**, 105232.

Jiao Y, Lee YK, Gladman N, *et al*. 2018. MSD1 regulates pedicellate spikelet fertility in sorghum through the jasmonic acid pathway. Nature Communications **9**, 822.

Jin Y, Luo Q, Tong H, *et al*. 2011. An AT-hook gene is required for palea formation and floral organ number control in rice. Developmental Biology **359**, 277–288.

Jing S, Jiang P, Sun X, Yu L, Wang E, Qin J, Zhang F, Prat S, Song B. 2023. Long-distance control of potato storage organ formation by SELF PRUNING 3D and FLOWERING LOCUS T-like 1. Plant Communications **4**, 100547.

Kaneko-Suzuki M, Kurihara-Ishikawa R, Okushita-Terakawa C, Kojima C, Nagano-Fujiwara M, Ohki I, Tsuji H, Shimamoto K, Taoka KI. 2018. TFL1-Like proteins in rice antagonize rice FT-Like protein in inflorescence development by competition for complex formation with 14-3-3 and FD. Plant and Cell Physiology **59**, 458–468.

Kawamoto N, Sasabe M, Endo M, Machida Y, Araki T. 2015. Calcium-dependent protein kinases responsible for the phosphorylation of a bZIP transcription factor FD crucial for the florigen complex formation. Scientific Reports **5**, 8341.

Khosa J, Bellinazzo F, Kamenetsky Goldstein R, Macknight R, Immink RGH. 2021. PHOSPHATIDYLETHANOLAMINE-BINDING PROTEINS: the conductors of dual reproduction in plants with vegetative storage organs. Journal of Experimental Botany **72**, 2845–2856.

Kim SH, Son GH, Bhattacharjee S, Kim HJ, Nam JC, Nguyen PDT, Hong JC, Gassmann W. 2014. The Arabidopsis immune adaptor SRFR1 interacts with TCP transcription factors that redundantly contribute to effector-triggered immunity. The Plant Journal **78**, 978–989.

Kitagawa S, Shimada S, Murai K. 2012. Effect of *Ppd-1* on the expression of flowering-time genes in vegetative and reproductive growth stages of wheat. Genes & Genetic Systems **87**, 161–168.

Knott JE. 1934. Effect of a localized photoperiod on spinach. Journal of the American Society for Horticultural Science **31**, 152–154.

Komiya R, Ikegami A, Tamaki S, Yokoi S, Shimamoto K. 2008. *Hd3a* and *RFT1* are essential for flowering in rice. Development **135**, 767–774.

Komiya R, Yokoi S, Shimamoto K. 2009. A gene network for long-day flowering activates *RFT1* encoding a mobile flowering signal in rice. Development **136**, 3443–3450.

Kosugi S, Ohashi Y. 1997. PCF1 and PCF2 specifically bind to cis elements in the rice proliferating cell nuclear antigen gene. The Plant Cell **9**, 1607–1619.

Krieger U, Lippman ZB, Zamir D. 2010. The flowering gene *SINGLE FLOWER TRUSS* drives heterosis for yield in tomato. Nature Genetics **42**, 459–463.

Kubota A, Ito S, Shim JS, *et al*. 2017. TCP4-dependent induction of *CONSTANS* transcription requires GIGANTEA in photoperiodic flowering in *Arabidopsis*. PLoS Genetics **13**, e1006856.

Leeggangers HA, Rosilio-Brami T, Bigas-Nadal J, *et al*. 2018. *Tulipa gesneriana* and *Lilium longiflorum PEBP* genes and their putative roles in flowering time control. Plant and Cell Physiology **59**, 90–106.

Li C, Dubcovsky J. 2008. Wheat FT protein regulates *VRN1* transcription through interactions with FDL2. The Plant Journal **55**, 543–554.

Li C, Gu M, Shi N, *et al*. 2011. Mobile *FT* mRNA contributes to the systemic florigen signalling in floral induction. Scientific Reports **1**, 73.

Li C, Lin H, Dubcovsky J. 2015. Factorial combinations of protein interactions generate a multiplicity of florigen activation complexes in wheat and barley. The Plant Journal **84**, 70–82.

Li C, Zhang K, Zeng X, Jackson S, Zhou Y, Hong Y. 2009. A *cis* element within *Flowering Locus T* mRNA determines its mobility and facilitates trafficking of heterologous viral RNA. Journal of Virology **83**, 3540–3548.

Li D, Zhang H, Mou M, Chen Y, Xiang S, Chen L, Yu D. 2019. Arabidopsis Class II TCP transcription factors integrate with the FT–FD module to control flowering. Plant Physiology **181**, 97–111.

Li K, Debernardi JM, Li C, Lin H, Zhang C, Jernstedt J, von Korff M, Zhong J, Dubcovsky J. 2021. Interactions between SQUAMOSA and SHORT VEGETATIVE PHASE MADS-box proteins regulate meristem transitions during wheat spike development. The Plant Cell **33**, 3621–3644.

Li X, Zhang G, Liang Y, Hu L, Zhu B, Qi D, Cui S, Zhao H. 2021. TCP7 interacts with Nuclear Factor-Ys to promote flowering by directly regulating *SOC1* in Arabidopsis. The Plant Journal **108**, 1493–1506.

Lifschitz E, Eshed Y. 2006. Universal florigenic signals triggered by *FT* homologues regulate growth and flowering cycles in perennial day-neutral tomato. Journal of Experimental Botany **57**, 3405–3414.

Lifschitz E, Eviatar T, Rozman A, Shalit A, Goldshmidt A, Amsellem Z, Alvarez JP, Eshed Y. 2006. The tomato *FT* ortholog triggers systemic signals that regulate growth and flowering and substitute for diverse environmental stimuli. Proceedings of the National Academy of Sciences, USA **103**, 6398–6403.

Liller CB, Neuhaus R, Von Korff M, Koornneef M, Van Esse W. 2015. Mutations in barley row type genes have pleiotropic effects on shoot branching. PLoS One **10**, e0140246.

Liu C, Teo ZWN, Bi Y, Song S, Xi W, Yang X, Yin Z, Yu H. 2013. A conserved genetic pathway determines inflorescence architecture in *Arabidopsis* and rice. Developmental Cell **24**, 612–622.

Liu J, Cheng X, Liu P, Li D, Chen T, Gu X, Sun J. 2017. MicroRNA319-regulated TCPs interact with FBHs and PFT1 to activate CO transcription and control flowering time in *Arabidopsis*. PLoS Genetics **13**, e1006833.

Liu L, Li C, Liang Z, Yu H. 2018. Characterization of multiple C2 domain and transmembrane region proteins in Arabidopsis. Plant Physiology **176**, 2119–2132.

Liu L, Li C, Teo ZWN, Zhang B, Yu H. 2019. The MCTP-SNARE complex regulates florigen transport in Arabidopsis. The Plant Cell **31**, 2475–2490.

Liu L, Liu C, Hou X, Xi W, Shen L, Tao Z, Wang Y, Yu H. 2012. FTIP1 is an essential regulator required for florigen transport. PLoS Biology **10**, e1001313.

Liu L, Zhang Y, Yu H. 2020. Florigen trafficking integrates photoperiod and temperature signals in Arabidopsis. Journal of Integrative Plant Biology **62**, 1385–1398.

Liu S, Sehgal SK, Li J, Lin M, Trick HN, Yu J, Gill BS, Bai G. 2013. Cloning and characterization of a critical regulator for preharvest sprouting in wheat. Genetics **195**, 263–273.

Lu K-J, Huang N-C, Liu Y-S, Lu C-A, Yu T-S. 2012. Long-distance movement of Arabidopsis *FLOWERING LOCUS T* RNA participates in systemic floral regulation. RNA Biology **9**, 653–662.

Lucero LE, Manavella PA, Gras DE, Ariel FD, Gonzalez DH. 2017. Class I and Class II TCP transcription factors modulate SOC1-dependent flowering at multiple levels. Molecular Plant **10**, 1571–1574.

Luo D, Carpenter R, Vincent C, Copsey L, Coen E. 1996. Origin of floral asymmetry in *Antirrhinum*. Nature **383**, 794–799.

Manassero NGU, Viola IL, Welchen E, Gonzalez DH. 2013. TCP transcription factors: architectures of plant form. BioMolecular Concepts **4**, 111–127.

Mathieu J, Warthmann N, Küttner F, Schmid M. 2007. Export of FT protein from phloem companion cells is sufficient for floral induction in *Arabidopsis*. Current Biology **17**, 1055–1060.

Maurya JP, Singh RK, Miskolczi PC, Prasad AN, Jonsson K, Wu F, Bhalerao RP. 2020. Branching regulator *BRC1* mediates photoperiodic control of seasonal growth in hybrid aspen. Current Biology **30**, 122–126. e2.

Mimida N, Kidou S-I, Iwanami H, Moriya S, Abe K, Voogd C, Varkonyi-Gasic E, Kotoda N, Näsholm T. 2011. Apple FLOWERING LOCUS T proteins interact with transcription factors implicated in cell growth and organ development. Tree Physiology **31**, 555–566.

Mizoguchi T, Wright L, Fujiwara S, *et al*. 2005. Distinct roles of GIGANTEA in promoting flowering and regulating circadian rhythms in Arabidopsis. The Plant Cell **17**, 2255–2270.

Mo W, Zhang J, Zhang L, *et al*. 2022. *Arabidopsis* cryptochrome 2 forms photobodies with TCP22 under blue light and regulates the circadian clock. Nature Communications **13**, 2631.

Molinero-Rosales N, Latorre A, Jamilena M, Lozano R. 2004. *SINGLE FLOWER TRUSS* regulates the transition and maintenance of flowering in tomato. Planta **218**, 427–434.

Moraes TS, Immink RGH, Martinelli AP, Angenent GC, van Esse W, Dornelas MC. 2022. *Passiflora organensis FT/TFL1* gene family and their putative roles in phase transition and floral initiation. Plant Reproduction **35**, 105–126.

Morrell PL, Clegg MT. 2007. Genetic evidence for a second domestication of barley (*Hordeum vulgare*) east of the Fertile Crescent. Proceedings of the National Academy of Sciences, USA **104**, 3289–3294.

Mulki MA, von Korff M. 2016. CONSTANS controls floral repression by up-regulating *VERNALIZATION2* (*VRN-H2*) in barley. Plant Physiology **170**, 325–337.

Nakamura S, Abe F, Kawahigashi H, *et al*. 2011. A wheat homolog of MOTHER of FT and TFL1 acts in the regulation of germination. The Plant Cell **23**, 3215–3229.

Nath U, Crawford BCW, Carpenter R, Coen E. 2003. Genetic control of surface curvature. Science **299**, 1404–1407.

Navarro C, Abelenda JA, Cruz-Oró E, Cuéllar CA, Tamaki S, Silva J, Shimamoto K, Prat S. 2011. Control of flowering and recently reviewed in in potato by FLOWERING LOCUS T. Nature **478**, 119–122.

Nemoto Y, Nonoue Y, Yano M, Izawa T. 2016. *Hd1*, a *CONSTANS* ortholog in rice, functions as an *Ehd1* repressor through interaction with monocot-specific CCT-domain protein Ghd7. The Plant Journal **86**, 221–233.

Nicolas M, Cubas P. 2016a. TCP factors: new kids on the signaling block. Current Opinion in Plant Biology **33**, 33–41.

Nicolas M, Cubas P. 2016b. The role of TCP transcription factors in shaping flower structure, leaf morphology, and plant architecture. In: Gonzalez DH, ed. Plant Transcription factors. Boston: Academic Press, 249–267.

Nicolas M, Torres-Pérez R, Wahl V, *et al*. 2022. Spatial control of potato tuberization by the TCP transcription factor BRANCHED1b. Nature Plants **8**, 281–294.

Niwa M, Daimon Y, Kurotani K, *et al*. 2013. BRANCHED1 interacts with FLOWERING LOCUS T to repress the floral transition of the axillary meristems in *Arabidopsis*. The Plant Cell **25**, 1228–1242.

Pankin A, Altmüller J, Becker C, von Korff M. 2018. Targeted resequencing reveals genomic signatures of barley domestication. New Phytologist **218**, 1247–1259.

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.

Peleg Z, Fahima T, Korol AB, Abbo S, Saranga Y. 2011. Genetic analysis of wheat domestication and evolution under domestication. Journal of Experimental Botany **62**, 5051–5061.

Périlleux C, Huerga-Fernández S. 2022. Reflections on the triptych of meristems that build flowering branches in tomato. Frontiers in Plant Science **13**, 798502.

Pittendrigh CS, Minis DH. 1964. The entrainment of circadian oscillations by light and their role as photoperiodic clocks. The American Naturalist **98**, 261–294.

Plantenga FDM, Bergonzi S, Abelenda JA, Bachem CWB, Visser RGF, Heuvelink E, Marcelis LFM. 2019. The tuberization signal StSP6A represses flower bud development in potato. Journal of Experimental Botany **70**, 937–948.

Plantenga FDM, Siakou M, Bergonzi S, Heuvelink E, Bachem CWB, Visser RGF, Marcelis LFM. 2016. Regulating flower and tuber formation in potato with light spectrum and day length. Acta Horticulturae **1134**, 267–276.

Pnueli L, Carmel-Goren L, Hareven D, Gutfinger T, Alvarez J, Ganal M, Zamir D, Lifschitz E. 1998. The *SELF-PRUNING* gene of tomato regulates vegetative to reproductive switching of sympodial meristems and is the ortholog of *CEN* and *TFL1*. Development **125**, 1979–1989.

Pnueli L, Gutfinger T, Hareven D, Ben-Naim O, Ron N, Adir N, Lifschitz E. 2001. Tomato SP-interacting proteins define a conserved signaling system that regulates shoot architecture and flowering. The Plant Cell **13**, 2687–2702.

Poets AM, Fang Z, Clegg MT, Morrell PL. 2015. Barley landraces are characterized by geographically heterogeneous genomic origins. Genome Biology **16**, 1–11.

Ramsay L, Comadran J, Druka A, *et al*. 2011. *INTERMEDIUM-C*, a modifier of lateral spikelet fertility in barley, is an ortholog of the maize domestication gene *TEOSINTE BRANCHED 1*. Nature Genetics **43**, 169–172.

Rath M, Challa KR, Sarvepalli K, Nath U. 2022. CINCINNATA-Like TCP transcription factors in cell growth – an expanding portfolio. Frontiers in Plant Science **13**, 825341.

Rodríguez-Falcón M, Bou J, Prat S. 2006. Seasonal control of tuberization in potato: conserved elements with the flowering response. Annual Review of Plant Biology **57**, 151–180.

Ryu C-H, Lee S, Cho L-H, *et al*. 2009. *OsMADS50* and *OsMADS56* function antagonistically in regulating long day (LD)-dependent flowering in rice. Plant, Cell & Environment **32**, 1412–1427.

Shaw LM, Lyu B, Turner R, Li C, Chen F, Han X, Fu D, Dubcovsky J. 2019. *FLOWERING LOCUS T2* regulates spike development and fertility in temperate cereals. Journal of Experimental Botany **70**, 193–204.

Shaw LM, Turner AS, Herry L, Griffiths S, Laurie DA. 2013. Mutant alleles of *Photoperiod-1* in wheat (*Triticum aestivum* L.) that confer a late flowering phenotype in long days. PLoS One **8**, e79459.

Silva GFF, Silva EM, Correa JPO, *et al*. 2019. Tomato floral induction and flower development are orchestrated by the interplay between gibberellin and two unrelated microRNA-controlled modules. New Phytologist **221**, 1328–1344.

Soyk S, Müller NA, Park SJ, Schmalenbach I, Jiang K, Hayama R, Zhang L, Van Eck J, Jiménez-Gómez JM, Lippman ZB. 2017. Variation in the flowering gene *SELF PRUNING 5G* promotes day-neutrality and early yield in tomato. Nature Genetics **49**, 162–168.

Spooner DM, McLean K, Ramsay G, Waugh R, Bryan GJ. 2005. A single domestication for potato based on multilocus amplified fragment length polymorphism genotyping. Proceedings of the National Academy of Sciences, USA **102**, 14694–14699.

Sun J, Bie XM, Chu XL, Wang N, Zhang XS, Gao X-Q. 2023. Genome-edited *TaTFL1-5* mutation decreases tiller and spikelet numbers in common wheat. Frontiers in Plant Science **14**, 1142779.

Sun K, Huang M, Zong W, *et al*. 2022. *Hd1*, *Ghd7*, and *DTH8* synergistically determine the rice heading date and yield-related agronomic traits. Journal of Genetics and Genomics **49**, 437–447.

Sun Y, Jia X, Yang Z, Fu Q, Yang H, Xu X. 2023. Genome-wide identification of PEBP gene family in *Solanum lycopersicum*. International Journal of Molecular Sciences **24**, 9185.

Susila H, Jurić S, Liu L, *et al*. 2021. Florigen sequestration in cellular membranes modulates temperature-responsive flowering. Science **373**, 1137–1142.

Susila H, Purwestri YA. 2023. PEBP signaling network in tubers and tuberous root crops. Plants **12**, 264.

Takada S, Goto K. 2003. TERMINAL FLOWER2, an Arabidopsis homolog of Heterochromatin Protein1, counteracts the activation of *FLOWERING LOCUS T* by CONSTANS in the vascular tissues of leaves to regulate flowering time. The Plant Cell **15**, 2856–2865.

Takeda T, Suwa Y, Suzuki M, Kitano H, Ueguchi-Tanaka M, Ashikari M, Matsuoka M, Ueguchi C. 2003. The *OsTB1* gene negatively regulates lateral branching in rice. The Plant Journal **33**, 513–520.

Tamaki S, Matsuo S, Wong HL, Yokoi S, Shimamoto K. 2007. Hd3a protein is a mobile flowering signal in rice. Science **316**, 1033–1036.

Taoka KI, Ohki I, Tsuji H, *et al*. 2011. 14-3-3 proteins act as intracellular receptors for rice Hd3a florigen. Nature **476**, 332–335.

Teo C-J, Takahashi K, Shimizu K, Shimamoto K, Taoka K. 2017. Potato tuber induction is regulated by interactions between components of a tuberigen complex. Plant and Cell Physiology **58**, 365–374.

Turner A, Beales J, Faure S, Dunford RP, Laurie DA. 2005. The pseudo-response regulator *Ppd-H1* provides adaptation to photoperiod in barley. Science **310**, 1031–1034.

Turner AS, Faure S, Zhang Y, Laurie DA. 2013. The effect of day-neutral mutations in barley and wheat on the interaction between photoperiod and vernalization. Theoretical and Applied Genetics. **126**, 2267–2277.

Urano K, Maruyama K, Koyama T, Gonzalez N, Inzé D, Yamaguchi-Shinozaki K, Shinozaki K. 2022. CIN-like TCP13 is essential for plant growth regulation under dehydration stress. Plant Molecular Biology **108**, 257–275.

van Es SW, Muñoz-Gasca A, Romero-Campero FJ, *et al*. 2024. A gene regulatory network critical for axillary bud dormancy directly controlled by Arabidopsis BRANCHED1. New Phytologist **241**, 1193–1209.

Vicentini G, Biancucci M, Mineri L, Chirivì D, Giaume F, Miao Y, Kyozuka J, Brambilla V, Betti C, Fornara F. 2023. Environmental control of rice flowering time. Plant Communications **4**, 100610.

Viola IL, Alem AL, Jure RM, Gonzalez DH. 2023. Physiological roles and mechanisms of action of class I TCP transcription factors. International Journal of Molecular Sciences **24**, 5437.

Viola IL, Gonzalez DH. 2023. TCP transcription factors in plant reproductive development: juggling multiple roles. Biomolecules **13**, 750.

Wang S, Yang X, Xu M, *et al*. 2015. A rare SNP identified a TCP transcription factor essential for tendril development in cucumber. Molecular Plant **8**, 1795–1808.

Wang X, Gao J, Zhu Z, Dong X, Wang X, Ren G, Zhou X, Kuai B. 2015. TCP transcription factors are critical for the coordinated regulation of *ISOCHORISMATE SYNTHASE 1* expression in *Arabidopsis thaliana*. The Plant Journal **82**, 151–162.

Wang Z, Cui D, Liu C, Zhao J, Liu J, Liu N, Tang D, Hu Y. 2019. TCP transcription factors interact with ZED1-related kinases as components of the temperature-regulated immunity. Plant, Cell & Environment **42**, 2045–2056.

Whipple CJ, Kebrom TH, Weber AL, Yang F, Hall D, Meeley R, Schmidt R, Doebley J, Brutnell TP, Jackson DP. 2011. *grassy tillers1* promotes apical dominance in maize and responds to shade signals in the grasses. Proceedings of the National Academy of Sciences, USA **108**, E506–E512.

Wigge PA, Kim MC, Jaeger KE, Busch W, Schmid M, Lohmann JU, Weigel D. 2005. Integration of spatial and temporal information during floral induction in *Arabidopsis*. Science **309**, 1056–1059.

Wu J-F, Tsai H-L, Joanito I, *et al*. 2016. LWD–TCP complex activates the morning gene *CCA1* in *Arabidopsis*. Nature Communications **7**, 13181.

Xi W, Liu C, Hou X, Yu H. 2010. *MOTHER OF FT AND TFL1* regulates seed germination through a negative feedback loop modulating ABA signaling in *Arabidopsis*. The Plant Cell **22**, 1733–1748.

Yamaguchi A, Kobayashi Y, Goto K, Abe M, Araki T. 2005. *TWIN SISTER OF FT* (*TSF*) acts as a floral pathway integrator redundantly with *FT*. Plant and Cell Physiology **46**, 1175–1189.

Yan L, Loukoianov A, Blechl A, Tranquilli G, Ramakrishna W, SanMiguel P, Bennetzen JL, Echenique V, Dubcovsky J. 2004. The wheat *VRN2* gene is a flowering repressor down-regulated by vernalization. Science **303**, 1640–1644.

Yu Z, Chen W, Wang Y, Zhang P, Shi N, Hong Y. 2022. Mobile flowering locus T RNA – biological relevance and biotechnological potential. Frontiers in Plant Science **12**, 792192.

Zeevaart JA. 2008. Leaf-produced floral signals. Current Opinion in Plant Biology **11**, 541–547.

Zhan W, Cui L, Guo G, Zhang Y. 2023. Genome-wide identification and functional analysis of the *TCP* gene family in rye (*Secale cereale* L.). Gene **854**, 147104.

Zhang B, Li C, Li Y, Yu H. 2020. Mobile TERMINAL FLOWER1 determines seed size in *Arabidopsis*. Nature Plants **6**, 1146–1157.

Zhang B, Liu H, Qi F, Zhang Z, Li Q, Han Z, Xing Y. 2019. Genetic interactions among *Ghd7*, *Ghd8*, *OsPRR37* and *Hd1* contribute to large variation in heading date in rice. Rice **12**, 48.

Zhang G, Jin X, Li X, Zhang N, Li S, Si H, Rajora OP, Li X-Q. 2022. Genome-wide identification of PEBP gene family members in potato, their phylogenetic relationships, and expression patterns under heat stress. Molecular Biology Reports **49**, 4683–4697.

Zhang J, Zhou X, Yan W, *et al*. 2015. Combinations of the *Ghd7*, *Ghd8* and *Hd1* genes largely define the ecogeographical adaptation and yield potential of cultivated rice. New Phytologist **208**, 1056–1066.

Zhang S, Hu W, Wang L, Lin C, Cong B, Sun C, Luo D. 2005. *TFL1/CEN*-like genes control intercalary meristem activity and phase transition in rice. Plant Science **168**, 1393–1408.

Zhang X, Campbell R, Ducreux LJM, *et al*. 2020. TERMINAL FLOWER-1/CENTRORADIALIS inhibits tuberisation via protein interaction with the tuberigen activation complex. The Plant Journal **103**, 2263–2278.

Zhang Z, Hu W, Shen G, Liu H, Hu Y, Zhou X, Liu T, Xing Y. 2017. Alternative functions of Hd1 in repressing or promoting heading are determined by Ghd7 status under long-day conditions. Scientific Reports **7**, 5388.

Zhao X, Guo Y, Kang L, *et al*. 2023. Population genomics unravels the Holocene history of bread wheat and its relatives. Nature Plants **9**, 403–419.

Zhou H, Hwarari D, Ma H, Xu H, Yang L, Luo Y. 2022. Genomic survey of TCP transcription factors in plants: phylogenomics, evolution and their biology. Frontiers in Genetics **13**, 1060546.

Zhu W, Yang L, Wu D, *et al*. 2021. Rice *SEPALLATA* genes *OsMADS5* and *OsMADS34* cooperate to limit inflorescence branching by repressing the *TERMINAL FLOWER1*-like gene *RCN4*. New Phytologist **233**, 1682–1700.

Zhu Y, Klasfeld S, Jeong CW, Jin R, Goto K, Yamaguchi N, Wagner D. 2020. TERMINAL FLOWER 1-FD complex target genes and competition with FLOWERING LOCUS T. Nature Communications **11**, 5118.

Zhu Y, Liu L, Shen L, Yu H. 2016. NaKR1 regulates long-distance movement of FLOWERING LOCUS T in *Arabidopsis*. Nature Plants **2**, 16075

Zong W, Ren D, Huang M, *et al*. 2021. Strong photoperiod sensitivity is controlled by cooperation and competition among Hd1, Ghd7 and DTH8 in rice heading. New Phytologist **229**, 1635–1649.