Update on the Evolution of Temperature Regulated Flowering

Short title: Evolution of Temperature Regulated Flowering

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Title: Flowering Time Runs Hot and Cold

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[1]This work was supported by the USDA | National Institute of Food and Agriculture (NIFA; grant no. VT-H02712 to J.C.P.) and the Research Council Norway (grant no.301284 to S.F.)

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One-sentence summary: Recent advances in understanding the mechanisms underlying plant detection of and adaptation to different temperatures provides tools for breeding and management under global warming.

Author contributions: J.C.P. and S.F. both conceived of the research topic, performed the research, and wrote the paper.

Introduction

Variation in thermal climate is well known to shape plant distributions by differentially affecting traits that contribute to lifetime fitness (Lancaster and Humphreys, 2020; Huang et al., 2021). From an agricultural perspective, increasing ambient temperatures between approximately 12ºC to 27ºC tend to increase photosynthetic capacity, resulting in an overall increase in energy stores and plant biomass (Bernacchi et al., 2009; Wigge, 2013). However, the fact that temperatures outside this range can promote phase transitions between juvenile and adult, and adult vegetative and reproductive growth (hereafter flowering), means that simply increasing growth temperatures can lead to delays, or even low yields in the crop (e.g. leaves versus fruits and seeds) of interest. Understanding phylogenetic patterns of how plants respond to these different temperatures is becoming critically important as we strive to feed an expected population of around 9.7 billion by 2050 (UN-DESA-PD, 2019). This need is further amplified by global warming, where average temperatures will continue to rise over the next century, seasonal norms will be punctuated by severe weather events such as unseasonal frosts or droughts, and day-night temperature differentials will be weakened (Cox et al., 2020).

Research over the past 25 years has elucidated multiple genetic pathways – age, autonomous, gibberellin response, photoperiod, vernalization, and ambient temperature – that control flowering time (Simpson and Dean, 2002). All of these pathways converge on the floral pathway integrator gene *FLOWERING LOCUS T* (*FT*) to promote flower production broadly across angiosperms (Ballerini and Kramer, 2011). The complexity of flowering regulation likely emerges from the critical nature of matching reproductive development with the appropriate environmental conditions. Flowers are particularly susceptible to damage by abiotic and biotic stressors, and in many plants, require active pollinators for adequate seed set (Jagadish et al., 2016).

In addition to *FT*, deep functional conservation has been found for many genes within the photoperiod flowering pathway, such that switches between long-, short-, and neutral-day flowering are evolving largely through the rewiring of an ancient daylength gene network (Hayama and Coupland, 2004; Fjellheim and Preston, 2018). By contrast, support for shared derived temperature pathways is limited (but see Ruelens et al., 2013; Dixon et al., 2019), either

due to incomplete sampling and/or multiple independent origins, particularly of low temperature regulated flowering (Amasino 2005; Ream et al., 2012; Preston and Fjellheim 2020). Despite the potentially stressful nature of low and high temperatures, in many areas of the world these conditions preempt climates favorable to flowering; as such they can be used as cues to ready plants for reproduction. Vernalization – defined as an extended period of above freezing cold – for example, triggers many temperate plants to become competent to inductive signals that will later provoke flowering (Amasino, 2004). In turn, the ability to respond to vernalization is often age dependent, and it is becoming clear that the 'memory' of vernalization can be influenced by variation in both low and high temperatures (Zhou et al., 2013; Bouché et al., 2015).

Here, we provide an update on what is known about the mechanisms underlying temperature-regulated flowering time, their conservation, and their evolution at both the micro- and macro-scale. We will start with an appraisal of evidence for one or more plant thermal sensory systems and present the emerging picture for recruitment of functionally novel and ancient flowering time pathway genes in the rewiring or independent origins of ambient, low, and high temperature regulated phase change. We will focus on how plants have modified their sensitivities to differences in absolute temperatures, their duration and variation; and assess the importance of temperature fluctuations in determining plasticity in flowering time. As well as revealing areas of research required for a better understanding of how past thermal climates have shaped global patterns of plasticity in plant phase change, we will consider the implications for these phenological thermal responses in light of global warming.

THERMAL SENSING MECHANISMS IN PLANTS ARE STILL BEING DISCOVERED

In addition to being distributed across a broad spectrum of climate zones, from tropical lowland to temperate and cold desert (Geiger, 1954; Beck et al., 2018), individual plants experience changes in temperature that mark different seasons, day to night cycles, and even the rapid cooling of solar irradiation caused by a sudden breeze (Fig. 1) (McClung and Davis, 2010). Although these changes in temperature are likely to affect cellular physiology in different ways (e.g. by altering membrane fluidity and protein folding), they are hypothesized to integrate into bona fide thermal sensory systems, allowing for active signal transduction and downstream

responses (Lamers et al., 2020). Primary thermal sensors can be defined as those that show short term alterations in structure or activity directly in response to changes in external temperature, and that continually transduce signals to the plant to foster longer term responses such as temperature acclimation, flowering competency, and floral induction (Vu et al., 2019; Lamers et al., 2020). Current data suggest distinct thermal sensors for ambient, low, and high temperatures that affect different combinations of downstream signaling pathways, and ultimately growth and development (Lamers et al., 2020). A number of conserved temperature sensing mechanisms have been proposed for seed plants, many of which have been reviewed previously (McClung and Davis, 2010; Guo et al., 2018), and will not be exhaustively discussed here. We will focus on thermal sensing mechanisms for which there is strongest evidence based on relatively recent work.

Ambient temperature sensing

At least some plants can detect subtle changes in ambient temperature through the thermal reversion of active (Pfr, far-red absorbing) to inactive (Pr, red absorbing) phytochromes (Casal and Questa, 2018). Most of the evidence for thermal reversion comes from work on PHYTOCHROME A (PHYA) and PHYB that are found broadly in seed plants (Mathews, 2010). However, although PHYA and PHYB are widely known as pigment-containing light sensors that interact with the circadian clock to set daily and annual rhythms, compelling evidence for their role in light-dependent thermal sensing is so far limited to eudicots (Jung et al., 2016; Klose et al., 2020; Cao et al., 2021). In Arabidopsis (*Arabidopsis thaliana*, Brassicaceae), increased temperatures positively affect the speed of thermal reversion, derepressing epidermal PHYTOCHROME INTERACTING FACTOR 4 (PIF4) that promotes shoot cell elongation and flowering, the latter through transcriptional regulation of the florigen *FT* (Fig. 2) (Kumar et al., 2012; Legris et al., 2016; Kim et al., 2020). In the daytime, PIF4 activity is stabilized by HEMERA (HRM), allowing thermoresponsiveness during both the light and dark (Qia et al., 2020).

Thermal reversion in Arabidopsis is also known to be repressed by PHOTOPERIODIC CONTROL OF HYPOCOTYL 1 (PCH1) and PHYTOCHROME-INTERACTING FACTOR 6 (PIF6) (Smith et al., 2017; Huang et al., 2019), whereas ARABIDOPSIS RESPONSE

REGULATOR 4 (ARR4) (Sweere et al., 2001) promotes it. Recently it was also found that the long-day photoperiod flowering pathway protein GIGANTEA (GI) mediates the photoperiodicity of thermal reversion by attenuating PIF4 function under long-days (Park et al., 2020). Despite this progress in understanding thermal sensing, it is not known how thermal reversion intersects with the ambient flowering time pathway (see next section and Outstanding Questions), where higher ambient temperatures often promote faster flowering (but see Verhage et al., 2017; del Olmo et al., 2019). Furthermore, the lack of evidence for phytochrome-regulated thermal reversion outside core eudicots, begs the question as to the conservation and number of origins of this sensing mechanism.

Low temperature sensing

Recent advances in elucidating the mechanisms involved in low temperature perception in plants highlight the potential involvement of changes in membrane fluidity, membrane protein activity, and thermal reversion (Fujii et al., 2017; Guo et al., 2018). For the latter, the same PHYB-mediated detection of ambient temperature change has been hypothesized for cooler temperatures. However, recent work on the maidenhair fern (*Adiantum capillus-veneris*) and the umbrella liverwort (*Marchantia polymorpha*) also implicate the blue-light receptor phototropin in the repositioning of chloroplast away from the cell surface at low temperatures, presumably to avoid light (Fujii et al., 2017). In the case of membrane fluidity, it is posited that low temperature-induced changes in plasma membranes cause the formation of cytoskeletal bundles that interact with calcium signaling to trigger a number of signal transduction pathways, including the C-repeat binding factor (CBF) pathway involved in rapid cold acclimation (Chinnusamy et al., 2010; Hafke et al., 2013; Liu et al. 2017; Zhang et al., 2020). A potential direct sensor of chilling in rice (*Oryza sativa*) is the membrane protein COLD1 that activates the GTPase activity of RICE G-PROTEIN ALPHA SUBUNIT1 (RGA1) (Ma et al., 2015). Together these proteins trigger a calcium influx, possibly by directly forming a calcium permeable channel, again leading to signal transduction of cold response genes. Future work is required to experimentally test if COLD1/RGA1 is indeed part of a calcium permeable channel, and to determine if this model extends beyond rice.

High-temperature sensing

High temperatures appear to be sensed broadly across plants by heat shock proteins (HSPs) that work as molecular chaperones for proteins disaggregated by heat and other stressors (Liberek et al., 2008; Boden et al., 2013). When the hydrophobic regions of water-soluble proteins are exposed by heat-induced unfolding, they attract hydrophobic residues of HSPs, and together these promote the action of heat shock factors (HSFs). HSFs bind to heat shock elements (HSEs) associated with transcription of several genes. These include those that contribute to an epigenetic memory of heat and auxin biosynthesis required for growth and possibly phase change (Li et al., 2018; Friedrich et al., 2021).

VARIATION IN AMBIENT TEMPERATURE SIGNALING AND RESPONSE

Conservation and diversification of ambient temperature-mediated phase change in the Brassicaceae

In many Arabidopsis accessions, warm temperatures can substitute for long-days to accelerate flowering, but the dual regulation of many ambient temperature-responsive genes/proteins by photoperiod highlights the close connection between these environmental signals (Klose et al., 2020). As previously mentioned, PIF4 is an important node in the Arabidopsis thermal sensing pathway, being stabilized as ambient temperatures increase and convert Pfr to its inactive Pr form. However, PIF4 protein also increases during Pfr degradation in the dark. The role of dark-stabilized PIF4 protein in flowering manifests through its transcriptional activation of FT (Fig. 2) (Wigge, 2013). At lower ambient temperatures in Arabidopsis, the PIF4 binding site of FT is blocked by an H2A.Z nucleosome, whereas at higher temperatures this block is lifted (Kumar et al., 2012). Interesting, although the PIF4-FT regulon is conserved in *Brassica rapa* (Brassicaceae), higher ambient temperatures actually increase histone H2A.Z levels at *B. rapa* FT, resulting in a negative relationship between temperature and flowering (de Olmo et al., 2019). Arabidopsis *PIF4* levels are also negatively regulated by the evening complex (EC) of EARLY FLOWERING 3 (ELF3), ELF4, and LUX ARRYTHMO (LUX) in a temperature-dependent manner (Fig. 2) (Silva et al., 2020). Recent evidence suggests that warm temperatures inhibit the EC complex from DNA-binding by reducing the localization of ELF3 to sub-nuclear foci, thus allowing PIF4 to interact with FT (Ronald et al., 2021). In addition to controlling

flowering time, it has been hypothesized that the increased activity of PIF4 with warming nights contributes to concomitant earlier flower bud opening (Jagadish et al. 2016). While intriguing, the potential mechanism for this remains largely unexplored.

A second major component of the ambient temperature pathway in both Arabidopsis and *Brassica* sp. is mediated by differential expression and splicing of transcription factors that regulate both repressors and promoters of flowering (Verhage et al., 2017). In the Arabidopsis Col-0 ecotype, FLOWERING CONTROL LOCUS A (FCA) produces four alternative splice forms, one of which (lambda) becomes dominant at higher ambient temperatures to specifically repress the flowering repressor *FLOWERING LOCUS C* (*FLC*) (Quesada et al., 2003). Likewise, at lower ambient temperatures, specific spliceforms of FLOWERING LOCUS M (FLM) and MADS AFFECTING FLOWERING 2 (MAF2) bind to SHORT VEGETATIVE PHASE (SVP) to form floral repressor complexes; at higher temperatures FLM-delta and MAF2var2 variants predominate and no longer bind strongly to SVP (Lee et al., 2013; Posé et al., 2013; Airoldi et al., 2015). The importance of FLM splicing for local adaptation is evident when comparing natural Arabidopsis accessions from cool temperate environments. For example, Killean-0 from Scotland contains an insertion in the first intron of *FLC* that results in lower abundance of the beta variant at lower temperatures, resulting in earlier flowering relative to Col-0 (Lutz et al., 2015). Although ambient temperature-regulated alternative splicing appears to be conserved between Arabidopsis and *Brassica*, partially through differential splicing of splicing-related genes, the exact targets of the spliceosome appear to be quite distinct even across ecotypes (Vertage et al., 2017).

Evidence for rewiring versus independent origins of ambient temperature-regulated flowering across angiosperms

Similar to the case in Brassicaceae, angiosperms more broadly show variation in how they respond to different ambient temperatures. For example, bunch-flowered daffodil (*Narcissus tazetta*; Amarylidaceae) is faster, and *Chrysanthemum* sp. (Asteraceae) and *Phalaenopsis aphrodite* (Orchidaceae) slower, in flowering with high ambient temperatures, respectively (An et al., 2011). Moreover, in many wheat (*Triticum* sp.) and barley (*Hordeum vulgare*) (Pooideae, Poaceae) cultivars, the relationship between ambient temperature and flowering is positive under

long-days, but negative under short-days (Hemming et al., 2012). Part of this variation might be due to differences in the range of temperatures that are stressful to each genotype, whereby the activation of stress response pathways can come at a cost to reproduction (Lin et al., 2019). Rewiring of ambient stress response pathways is also likely to play a major role, an understanding of which will require fundamental knowledge on how conserved the ambient flowering time pathway is across plants.

In monocots, knowledge on the genetic basis of ambient temperature-regulated phase change is best understood within grasses, such as sub-tropical rice, and temperate wheat and barley. However, many questions remain, from the sensor of ambient temperature change to the transduction pathways that reset whole plant physiology (see Outstanding Questions). As previously mentioned, the role of PHYB in temperature sensing has not been investigated in grasses, and no *PIF*-like genes have been functionally characterized to date (Cao et al., 2021). On the other hand, members of the grass EC, including ELF3, have been found to increase with high ambient temperatures in barley (Ford et al., 2016; Ejaz and von Korff, 2017). These data suggest divergence in high ambient temperature regulation of the EC between Arabidopsis where it is repressed, and barley where it is promoted. This is despite the fact that the targeted accessions from both species flowered faster at higher ambient temperatures under long days (Ejaz and von Korff, 2017; Ronald et al., 2021).

Two of the key genes that affect grass ambient temperature response in long days are the CCT domain-containing gene *PHOTOPERIOD 1* (*PPD-H1*) and the MADS-box *FRUITFULL* (*FUL*)-like gene *VERNALIZATION 1* (*VRN1*) (Ejaz and von Korff, 2017). PPD-H1 is often considered a repressor of flowering, as it forms a repressor complex with other CCT domain proteins, such as CONSTANS1 (CO1), CO2 and possibly VRN2 (Shaw et al., 2020). However, it is becoming increasingly clear that both photoperiod and temperature can modify these protein-protein interactions, turning the repressor complex into an activator complex (Zong et al., 2021). In barley, a functional *PPD-H1* allele is required to accelerate flowering at high ambient temperatures in long days (Ejaz and von Korff, 2017). This acceleration of flowering by PPD-H1 and the activator complex at higher ambient temperatures is exacerbated in a *vrn1* background, suggesting that the repression of functional *VRN1* transcripts by high ambient temperatures is

incomplete (Ejaz and von Korff, 2017). Under short days, ambient temperatures repress wheat and barley flowering through the VRN2-CCT domain repressor complex, and via a VRN2-independent pathway involving the MADS-box protein ODD SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1 LIKE 2 (ODDSOC2) (Hemming et al., 2012).

In addition to *PPD-H1* and *VRN1*-like genes, studies on the temperate grass *Brachypodium distachyon* (Pooideae) have revealed a role for *VERNALIZATION INSENSITIVE 3-LIKE 4* (*VIL4*) in the long day acceleration of flowering at low ambient temperatures (An et al., 2015). Similar to VIN3 in Arabidopsis, VIL4 works with the POLYCOMB REPRESSIVE COMPLEX 2 (PRC2) to H3K27 methylate its target genes. However, whereas the target of repression of AtVIN3 is the flowering repressor *FLC* that inhibits flowering in the absence of vernalizing temperatures, the BdVIL4 target is miR156 that works in the age pathway to delay the juvenile-to-adult onset that preempts the reproductive transition (An et al., 2015). Interestingly, transcription of miR156 actually increases at low ambient temperatures in Arabidopsis and the orchid *Phalaenopsis* (An et al., 2011), and two related proteins VIL2 and VIL3 in rice repress a different flowering time repressor in a temperature independent manner (Wang et al., 2013; Yang et al., 2013). These data demonstrate evolution of crosstalk between the age and ambient temperature pathways both outside and within grasses. Additionally, they tentatively suggest that ambient temperature-regulated flowering was an ancient innovation that has been repeatedly modified through continued adaptation and/or developmental system drift (True and Haag, 2001). The latter conclusion is consistent with angiosperms evolving in (sub)tropical environments where small fluctuations in ambient temperatures could have signaled oncoming seasonal shifts in precipitation (Wing and Boucher, 1998).

Another area of interest in both eudicot and monocot species is the role of ambient temperatures in synchronization of irregular seed production, or mast flowering, across large geographic areas. The delta T model proposes that mast flowering is induced when plants experience a positive difference between previous summer temperatures and the summer prior to that (Kelly et al., 2013). A testable mechanism for this summer memory has been proposed to be epigenetic, either through promotive epigenetic marks on flowering promoters (e.g. *FT*) or repressive marks on flowering repressors (e.g. *FLC*) (Fig. 3) (Samarth et al., 2020). If this memory can be

277 demonstrated broadly across masting species that represent over 37 angiosperm plant families
278 (Samarth et al., 2020) (see Outstanding Questions), it would be another example of plants
279 coopting a highly conserved mechanism in convergent trait evolution, and would parallel a
280 similar winter memory in temperate plants (Luo et al., 2020) (see next section).
281
282 **EVOLUTION OF COLD-RESPONSIVE FLOWERING**
283
284 In addition to variation in ambient temperatures, plants distributed in temperate and high latitude
285 areas experience dramatic seasonal shifts in temperature, whereby winter (and often autumn and
286 spring) temperatures drop below 15ºC (Fig. 1B) (Preston and Sandve, 2013; Casal and
287 Balasubramanian, 2019). Prior to the onset of freezing, many temperate taxa are made competent
288 to flower by vernalization that ready them into reproductive development quickly in the spring
289 (Chouard, 1960; Heide 1994)). Several studies have also proposed that low temperatures regulate
290 and activate flower formation, since some plants form flower buds during vernalization
291 (Chouard, 1960; Wang et al., 2009; Kemi et al., 2019; O'Neill et al., 2019; Soppe et al., 2021).
292 Furthermore, grapevine (*Vitis vinifera*), sweet cherry (*Prunus* sp.), and peach (*Prunus persica*)
293 plants form flower buds the year before flowering and require a cold period to flower (Engin and
294 Ünal, 2007; Carmona et al., 2008; Vimont et al., 2019). The lack of a sufficiently cold winter can
295 also reduce the quantity and quality of fruit production (Atkinson et al., 2013).
296
297 A number of lines of evidence suggest that vernalization responsiveness has evolved multiple
298 times independently in angiosperms (Preston and Sandve, 2013), such as at the base of Pooideae
299 grasses (Brooking and Jamieson, 2002; Schwartz et al., 2010; Fiil et al., 2011; Saisho et al.,
300 2011; McKeown et al., 2016), in the Brassicaceae (Stinchcombe et al., 2005), and within the
301 sugar beet (*Betula vulgaris*) family Amaranthaceae (Boudry et al., 2002). Less well examined is
302 the extent to which closely related taxa vary in their vernalization sensitivity and temperature
303 threshold; the relationship of this variation to climate of origin; and the genetic mechanisms
304 underlying this variation. In this section, we will briefly outline the molecular basis of
305 vernalization responsiveness in Arabidopsis and other species, and then turn to evidence for fine-
306 tuning of this winter memory within closely related taxa.
307

Molecular basis for vernalization responsiveness in the Brassicaceae

The molecular basis for vernalization responsiveness has been best described in Arabidopsis and the process is divided into three parts: initiation, memory and resetting (Fig. 4) (Song et al., 2012). These processes are largely modulated by modification of the flowering repressor *FLOWERING LOCUS C* (*FLC*) (Michaels and Amasino, 1999; Sheldon et al., 2000). Positive regulation of FLC requires functional *FRIGIDA* (*FRI*) alleles, protein products of which attract transcription factors and chromatin modifiers to the *FLC* promoter (Johanson *et al.*, 2000; Choi *et al.*, 2011). In individuals with a vernalization response, FRI activates *FLC* prior to vernalization, making plants incompetent to flower (Helliwell et al., 2006; Searle et al., 2006). During initiation of the vernalization response, silencing of *FLC* is facilitated by *COOLAIR*, a cold-induced RNA that is antisense to *FLC* mRNA (Swiezewski et al., 2009; Rosa et al., 2016). Splice variants of *COOLAIR* and/or other associated proteins interact with FRI to form nuclear condensates, which are sequestered away from the *FLC* promoter (Zhu et al., 2021). This initial loss of *FLC* transcriptional activation is reversible as the nuclear FRI condensates are reduced when returned to warm temperatures (Zhu et al. 2021).

Only following the initiation phase does prolonged exposure to cold induce epigenetic repression of *FLC* through a gradual switch from activate to repressed chromatin (reviewed in Hepworth and Dean 2015). This memory phase is facilitated by the plant homeodomain (PHD) polycomb repressive complex 2 (PRC2) that removes activating histone marks (i.e. H3K36me3) and adds repressive histone marks (i.e. H3K27me3) (Yang et al., 2014) (Figs. 3, 4). The PHD-PRC2 complex is recruited by the long non-coding RNA (lncRNA) COLD-ASSISTED INTRONIC NON-CODING RNA (COLDAIR) and directed to the FLC promoter by another lncRNA, COLD OF WINTER-INDUCED NON-CODING RNA FROM THE PROMOTER (COLDWRAP) (Swiezewski et al., 2009; Kim and Sung, 2017). Part of the PHD-PRC2 complex is VERNALIZATION INSENSITIVE 3 (VIN3) and VERNALIZATION 2 (VRN2) that are specifically induced transcriptionally by low temperatures (Sung and Amasino 2004; Wood et al., 2006; De Lucia et al 2008). Epigenetic silencing of *FLC* is stabilized when PHD-PRC2 increases H3K27me3 levels across the whole of *FLC* (Yang et al., 2014). At the tissue level, *FLC* is gradually repressed over time due to a cell-autonomous switch, causing progressively more cells to be in a stable, repressed state until saturation has been reached (Angel et al., 2011;

Angel et al., 2015). In this sense, the modified chromatin and its stabilization by COLDWRAP functions as a cold memory, even during warm periods.

Since Arabidopsis is an annual plant, resetting of *FLC* expression happens during embryogenesis and involves a series of events that switch the chromatin to an active state in each subsequent generation (Sheldon et al., 2008). Putative *FLC* orthologs are the main targets of the vernalization pathway in other Brassicaceae species too (Wang et al., 2009; Aikawa et al., 2010; Albani et al., 2012; Baduel et al., 2016; Lee et al., 2018; Kemi et al., 2019; Wang et al., 2020). However, in contrast to annual Brassicaceae species, FLC is reactivated following transfer back to warm conditions in perennial Brassicaceae such as *Arabis* sp. (Kiefer et al., 2017). This observation indicates a role for *FLC* in differentiating between different life-history forms. Furthermore, annual and perennial species of Arabidopsis differ in the age at which they become responsive to cold temperatures, with perennial species acquiring competency to flower later in life (Wang et al., 2011; Bergonzi et al., 2013).

Secondary cold thermosensors are distributed across several Brassicaceae regulatory networks

Primary thermosensory information acquired by plants across both short (e.g. intraday to diurnal) and long (e.g. seasonal to interannual) timescales must be continuously integrated and interpreted by secondary thermosensors, such that it elicits appropriate physiological and developmental responses. Recent work, combining lab and field studies with mathematical modeling in Arabidopsis (Antoniou-Kourounioiti et al., 2018; Hepworth et al., 2018; Zhao et al., 2020) suggests that secondary thermosensing is distributed across distinct molecular networks (Fig. 4). *FLC* and *VIN3* are central components of the secondary thermosensory machinery operating during vernalization, both being controlled by several independent thermosensory inputs operating on different time scales (Antoniou-Kourounioiti et al., 2018; Hepworth et al., 2018). The initial repression of *FLC* is independent of *VIN3* and involves COOLAIR (Swiezewski et al., 2009; Rosa et al., 2016), but *VIN3* soon responds to the absence of warm temperatures to also downregulate *FLC* (Hepworth et al., 2018). Over longer time periods of stable cold, the membrane-associated *NAC DOMAIN-CONTAINING PROTEIN 40 LIKE 8* (*NTL8*) slowly activates *VIN3* transcriptionally to cause its gradual accumulation (Fig. 4; Sung and Amasino

2004; De Lucia et al., 2008; Zhao et al., 2020). This accumulation contributes to the slow, low temperature controlled epigenetic silencing of *FLC* by the PHD-PRC2 complex. These separate inputs involving the absence of warmth and the progression of cold combine to inform the plants about seasonal progression. A similar, multi-pathway secondary thermosensing system has also been suggested for ambient temperature regulation of *FT* (Kinmonth-Schultz et al., 2018).

Evidence for rewiring versus independent origins of vernalization responsive flowering outside of Brassicaceae

In cereals of the grass subfamily Pooideae, major players in the control of vernalization-induced flowering are distinct from those in Brassicaceae (Fig. 4). However, some *FLC*-like genes have been found to be minor players in the Pooideae vernalization response (Ruelens et al., 2013), such as the short day flowering repressor *ODDSOC2* in wheat, barley, and *B. distachyon* that downregulates *FLOWERING PROMOTER FACTOR1* (*FPF1*)-like (Greenup et al., 2010; Sharma et al., 2017). The main repressor of flowering in cereals is the CCT domain protein VERNALIZATION 2 (VRN2) that works similarly to the MADS-box protein FLC to prevent precocious autumn flowering via repression of the *FT*-like gene *VRN3* (Fig. 4) (Yan et al., 2004; Dubcovsky et al., 2006; Trevaskis et al., 2006; Hemming et al., 2008). During vernalization, the previously mentioned flowering promoter *VRN1* is gradually transcriptionally activated through the replacement of repressive H3K27me3 marks with activating H3K4me3 marks, possibly stemming from a region in the first large intron (Fig. 3) (Oliver et al., 2009; Sasani et al., 2009; Oliver et al., 2013). VRN1 provides floral competency by repressing *VRN2*, and by forming a positive feedback loop whereby indirect upregulation of *VRN3* induces further *VRN1* expression (Yan et al., 2006; Shimada et al., 2009).

VRN1 is induced by cold across the Pooideae subfamily, which corresponds with an inferred early origin of vernalization responsiveness within this temperate clade (McKeown et al., 2016). A direct functional link has also been established between VRN1 and vernalization responsiveness in core Pooideae species beyond barley and wheat, such as in perennial ryegrass (*Lolium perenne*), timothy (*Phleum pratense*), and fescue (*Festuca pratensis*) (Petersen et al., 2004; Andersen et al., 2006; Seppänen et al., 2010; Ergon et al., 2013), and in the non-core Pooideae taxon *B. distachyon* (Ream et al., 2014). In contrast, although *VRN2* expression is

induced by long days across Pooideae and its protein product represses flowering, VRN1 only appears to downregulate *VRN2* within core Pooideae (Ream et al., 2014; Woods et al., 2016; Xu and Chong, 2018; Sharma et al., 2020). Indeed, in *B. distachyon* REPRESSOR OF VERNALIZATION 1 (RVR1) rather than VRN2 is required for H3K27me3-induced *VRN1* repression during autumn (Woods et al., 2017).

Despite its closer relationship to Brassicaceae than Poaceae, a recent study investigating *Carthamus tinctorius* (safflower, Asteraceae) found that a *VRN1*-like gene (*CtFUL*) is also upregulated with *CtFT* in vernalization responsive ('winter'), but not vernalization unresponsive ('spring'), cultivars (Cullerne et al., 2021). Interestingly, two *FLC*-like genes *CtMAF1* and *CtMAF2* are also differentially expressed between winter and spring lines, but opposite to what might be predicted; their expression increases with cold for the winter cultivar. This observation contrasts with closely related chicory (*Cichorium intybus*), where an *FLC* homolog, *CiFL1*, is downregulated with cold temperatures (Périlleux et al., 2013). In sugar beet, diversification of two antagonistic *FT*-like genes have been implicated in the vernalization response (Pin et al., 2010). Taken together, these data suggest the cooption of a similar set of ancestral reproductive development genes (i.e. *MAF*-like, *FUL*-like, CCT domain, and *FT*-like) multiple times in the cold adapted flowering of angiosperms. Unlike the case of the ambient temperature pathway, where developmental system drift from an ancient pathway might be invoked, an ancient origin of vernalization responsive flowering seems unlikely given that cool-seasonal climates emerged only in the last 36 million years (Zachos et al., 2001; Preston and Sandve, 2013; Preston and Fjellheim, 2020).

Variation in vernalization sensitivity

Some plants display an absolute requirement for vernalization, in that they fail to flower entirely without cold. Others simply flower later if unvernalized (Amasino, 2004). Either way, the vernalization response is considered saturated when plants do not flower faster with longer vernalization periods. The required time to saturate vernalization varies depending on a plant's local environment and genotype. For example, a latitudinal cline in vernalization sensitivity has been identified across wide geographic scales in both Arabidopsis and sugar beet, with northern populations requiring longer vernalization than southern populations to saturate their requirement

(Boudry et al., 2002; Stinchcombe et al., 2005). Latitudinal differences in vernalization sensitivity have been linked to variation in initial *FLC* levels (Hepworth et al., 2020), as well as differential rates of epigenetic silencing of *FLC* (Shindo et al., 2006). While latitudinal clines are considered an indicator of adaptation, further studies are required to link the actual climatic variables (e.g. length of the growing period and temperature seasonality; Fig. 1) to variation in saturation times.

Despite correlations between latitude and vernalization sensitivity across wide geographic distances, evidence is lacking for this relationship at more local scales. In Arabidopsis, rather than showing latitudinal clines, populations at the northern edge of the range exposed to continental climates are more sensitive to vernalization than populations from oceanic climates (Shindo et al., 2006; Lewandowska-Sabat et al., 2012) (Fig. 5). A possible explanation for this pattern is that winter temperatures are more variable in coastal versus continental regions, and thus a longer duration of vernalization is required to both saturate the vernalization response and predict the real onset of spring (Lewandowska-Sabat et al., 2012; Zhao et al., 2020). To test this hypothesis, fine-scale data to determine winter temperature variability will be required for a variety of regions and plant taxa (see Outstanding Questions).

Temperature thresholds for vernalization

Previous studies have reported that vernalization in germinated plants is optimal at around 5-10°C (Atherton et al., 1990; Rawson et al., 1998; Brooking and Jamieson, 2002; Wollenberg and Amasino, 2012; Ream et al., 2014; Duncan et al., 2015; Cullerne et al., 2021). At 0°C and above 15°C, vernalization efficiency is greatly attenuated [but see Niu et al., 2004; Cullerne et al., 2021). However, even given a maximum vernalization temperature, vernalization is still efficient across a range of temperatures, highlighting the ability of plants to respond to and buffer against a range of temperatures over diurnal, seasonal, and annual timescales. The fact that vernalization is less efficient below 5°C indicates that in more northern climates of the northern hemisphere vernalization response will mainly be saturated in the cool autumn months prior to winter itself (Duncan et al., 2015; Hepworth et al., 2020). The saturation of vernalization response before snow cover is linked to early flower production in the spring, possibly to avoid herbivory (Duncan et al., 2015). Whether fine-tuning of temperature sensitivity and vernalization saturation

can keep up with ongoing climate change is an open question. The answer will require knowledge of variation in flowering behavior at both the intra- and interspecific level.

THE IMPACT OF HIGH TEMPERATURES ON FLOWERING

Heat stress-induced flowering

'Stressful' high temperatures can be defined by their negative impacts on growth and yield, and vary in their lower limits based on the taxon of interest. For example, growth is entirely blocked at 25°C in temperate broccoli (*Brassica oleracea*) and at 38°C in sub-tropical maize (*Zea mays*) (Hatfield and Prueger, 2015). A delay or succession of growth at high temperatures can indirectly increase days to flowering, but studies in Arabidopsis and wheat suggest variation in developmentally (e.g. leaf number)-based flowering time is dependent on genotype (Balasubramanian et al., 2006; Posé et al., 2013; Dixon et al., 2019). Although few studies have quantified plant flowering time responses to a range of high temperatures (see Outstanding Questions), stress in general is known to promote flowering across a diversity of angiosperms, presumably as a means of reproductive assurance (Takeno, 2016). It is likely that a generic stress response pathway for flowering exists that incorporates signals such as growth and cellular damage. However, the importance of heat-specific signals on flowering, such as protein denaturation and the concomitant activation of HSPs, largely remains to be elucidated.

High temperatures devernalize plants

It has long been known that in some vernalization responsive plants high temperatures can remove the memory of winter and cause 'devernalization'. For example, exposure of winter rye (*Secale cereale*; Poaceae) to 35°C for different lengths of time following vernalization leads to a progressive reversal of the vernalization response (Purvis and Gregory, 1945). A similar response has also been identified in Arabidopsis (Bouche *et al.*, 2015; Périlleux *et al.*, 2013; Shindo *et al.*, 2006), chicory (Périlleux *et al.*, 2013) and wheat (Dixon *et al.*, 2019). However, in Arabidopsis and chicory, stabilizing the plants at 20°C before transferring them to 30+°C effectively prevents devernalization (Périlleux et al., 2013; Bouché et al., 2015).

493 The molecular basis of devernalization appears to be the remodeling of chromatin at
494 vernalization response loci, such as the removal of repressive H3K27me3 marks on Arabidopsis
495 *FLC* and histone deacetylation at cereal grass *VRN1* (Fig. 3) (Oliver et al., 2013; Bouché et al.,
496 2015). This resetting is akin to that occurring in germline cells and post-flowering meristems in
497 annuals and perennials, respectively. However, much is still to be learned about whether a
498 devernalization response necessarily follows from a vernalization response, the degree of
499 conservation of the devernalization response across angiosperms, and whether this response
500 evolved from a common high temperature-mediated flowering pathway. From a more ecological
501 perspective, it is also unclear whether the loss of winter memory through devernalization is
502 adaptive (see Outstanding Questions). An adaptive explanation seems particularly questionable
503 given that prolonged high temperatures are unusual during temperate autumns and winters, and
504 that only long daily periods of low temperatures are vernalizing (Chujo, 1966). On the other
505 hand, the study of vernalization and devernalization responses has so far been limited to a few
506 taxa and experimental conditions, and is expected to become more pertinent as extreme weather
507 events become more of the norm (Neilson et al., 2020).
508
509 **FLOWERING TIME IN THE CONTEXT OF GLOBAL WARMING: FUTURE**
510 **DIRECTIONS**
511
512 As the climate changes and extreme weather events become more common (Neilson et al.,
513 2020), an understanding of the intersection between low and high temperatures on flowering
514 time across a range of taxa, and in more natural settings, will be important for conservation
515 planning and crop breeding. As reviewed above, most of our understanding of temperature-
516 induced flowering has focused on temperate species, specifically in relation to vernalizing
517 conditions. Although much remains unknown about variation in the vernalization response in
518 relation to how it is sensed, its temperature threshold, and its saturation time, an even greater
519 knowledge gap remains in how ambient to high temperatures affect flowering outside of
520 Arabidopsis (see Outstanding Questions). In tropical species, for example, global warming by a
521 few degrees might shift, lengthen, or shorten flowering time, particularly if species are close to
522 their upper thermal limits (Kingsolver, 2009; but see Pau et al., 2013). The potential of a high
523 temperature memory of summer is also an intriguing hypothesis, as is the idea that a temperature

memory could span multiple seasons in perennial taxa (Fig. 4) (Samarth et al., 2020; see Outstanding Questions). Exploration of these issues will require a concerted effort by the plant biology community at multiple taxonomic, geographical, and organizational scales, as well as an eye to more 'natural' lab conditions.

Advances

- Much recent progress has been made in determining the sensing mechanisms for ambient, low, and high temperatures, particularly within core eudicots.
- Flowering responses to different temperatures are broadly mediated by long non-coding RNAs, differential splicing, and chromatin modifications.
- Annual and perennial plants can be distinguished by the reset time of their winter memory and the age to which they become vernalization responsive.
- Vernalization responsiveness has evolved multiple times through the recruitment of a conserved set of genes involved in reproductive development.

Outstanding Questions

- Are phytochromes involved in temperature sensing outside core eudicots?
- How does the thermal reversion pathway intersect with the ambient temperature flowering pathway?
- How have ambient stress response pathways been rewired to affect different ambient temperature flowering responses across angiosperms?
- Do plants have a summer memory? Does it involve the same epigenetic modifications as the winter memory?
- How important is variation in autumn-winter temperatures in shaping the evolution of vernalization saturation times?
- How variable are vernalization temperature thresholds within and between species? What ecological factors drive these patterns?
- Is there a heat stress flowering pathway? Is it conserved across angiosperms?
- Are all vernalization responsive plants devernalizable and is this response to seasonally unusual high temperatures adaptive?

Funding information

This work was supported by a National Science Foundation award (NSF-2120732 to JCP) and a Research Council Norway award (301284 to SF).

Figure Legends

Fig. 1: Climate maps showing global variation in the length of growing seasons and seasonal variation in temperature. (A) Temperature seasonality based on the standard deviation of monthly temperature (ºC) x 100 (BIO4). Red indicates high; blue indicates low. (B) Length of the growing season in the northern and southern hemispheres as depicted by the last month of the year with temperatures at or above 15ºC. Both datasets were obtained from the https://www.worldclim.org (Fick and Hijmans, 2017).

Fig. 2: Simplified genetic pathway for ambient temperature sensing and flowering response in Arabidopsis. Plant temperature sensing occurs, at least in part, through the regulation of genes also involved in the light-sensing and the circadian clock. Solid lines indicate well established connections, whereas dashed lines show hypothetical connections. Arrowheads denote positive regulation; bars denote negative regulation.

Fig. 3: Known and hypothetical temperature-mediated epigenetic modifications in cereal grasses, Arabidopsis, and masting plants.

Fig. 4: Similarities and differences in the vernalization genetic flowering pathway between cereal grasses and Arabidopsis. The Arabidopsis vernalization pathway occurs in three inter-dependent stages: initiation, memory, and resetting. Solid lines indicate well established connections, whereas dashed lines show hypothetical connections. Arrowheads denote positive regulation; bars denote negative regulation.

Fig. 5: Association between coastal-continental habitats and vernalization saturation time in Norwegian populations of Arabidopsis. Larger bluer circles denote population with higher

586 vernalization sensitivity, whereas smaller redder circles denote populations with lower
587 vernalization sensitivity. Land areas are colored based on Köppen climate classifications (Beck
588 et al., 2018).
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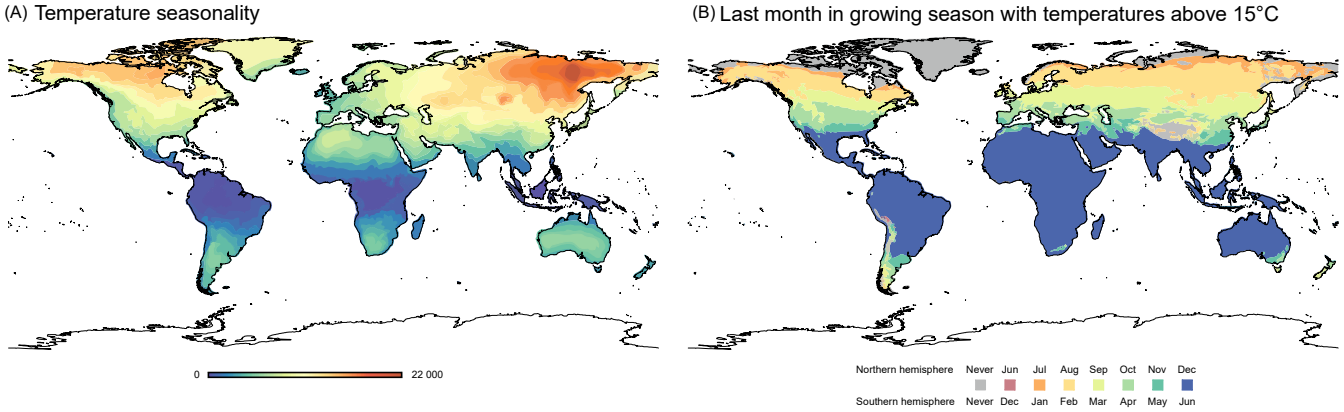
(A) Temperature seasonality
0
22 000
(B) Last month in growing season with temperatures above 15°C
Northern hemisphere
Never
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Southern hemisphere
Never
Dec
Jan
Feb
Mar
Apr
May
Jun

Fig 1

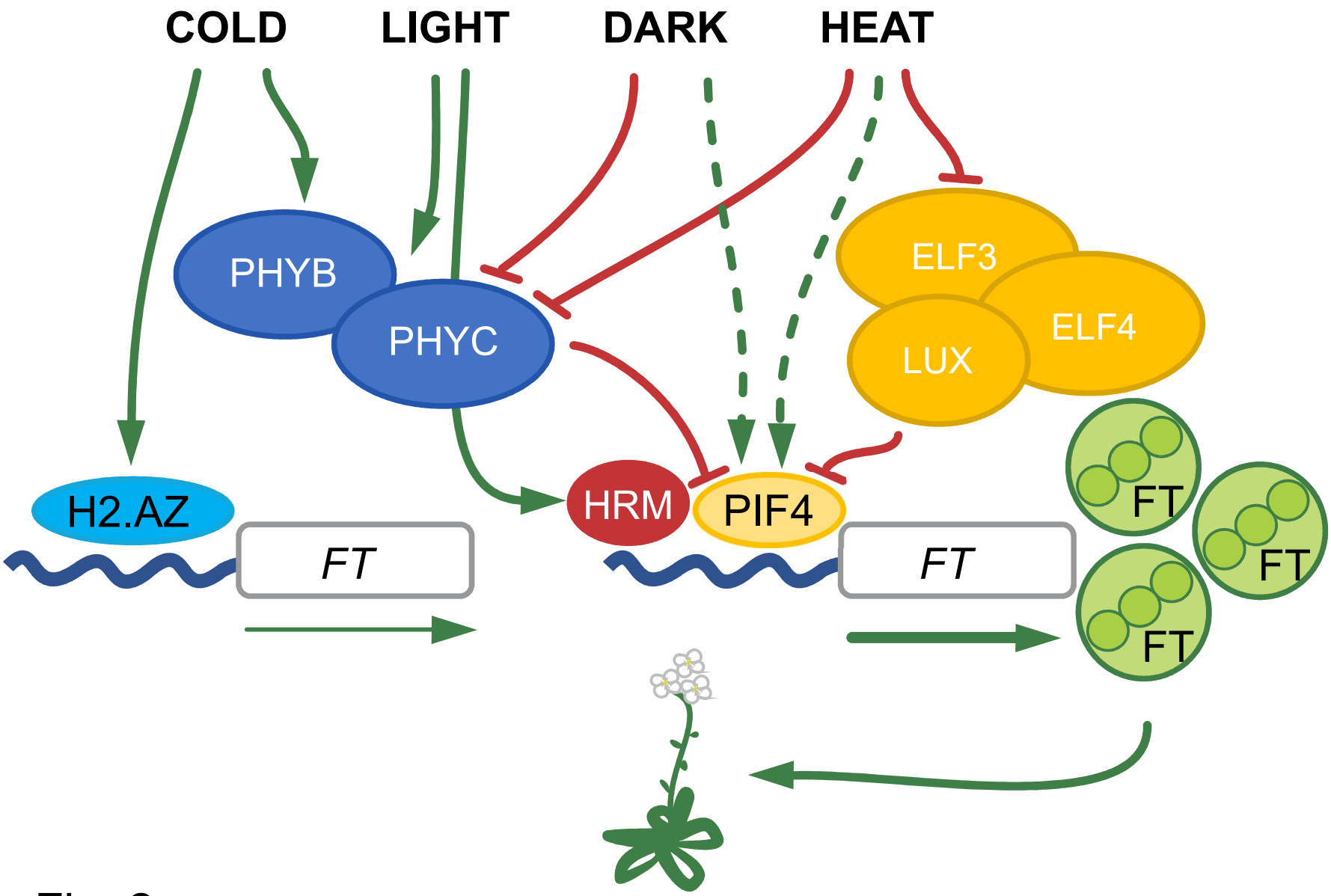
COLD
LIGHT
DARK
HEAT
PHYB
PHYC
ELF3
ELF4
LUX
H2.AZ
HRM
PIF4
FT
FT
FT
FT
FT

Fig. 2

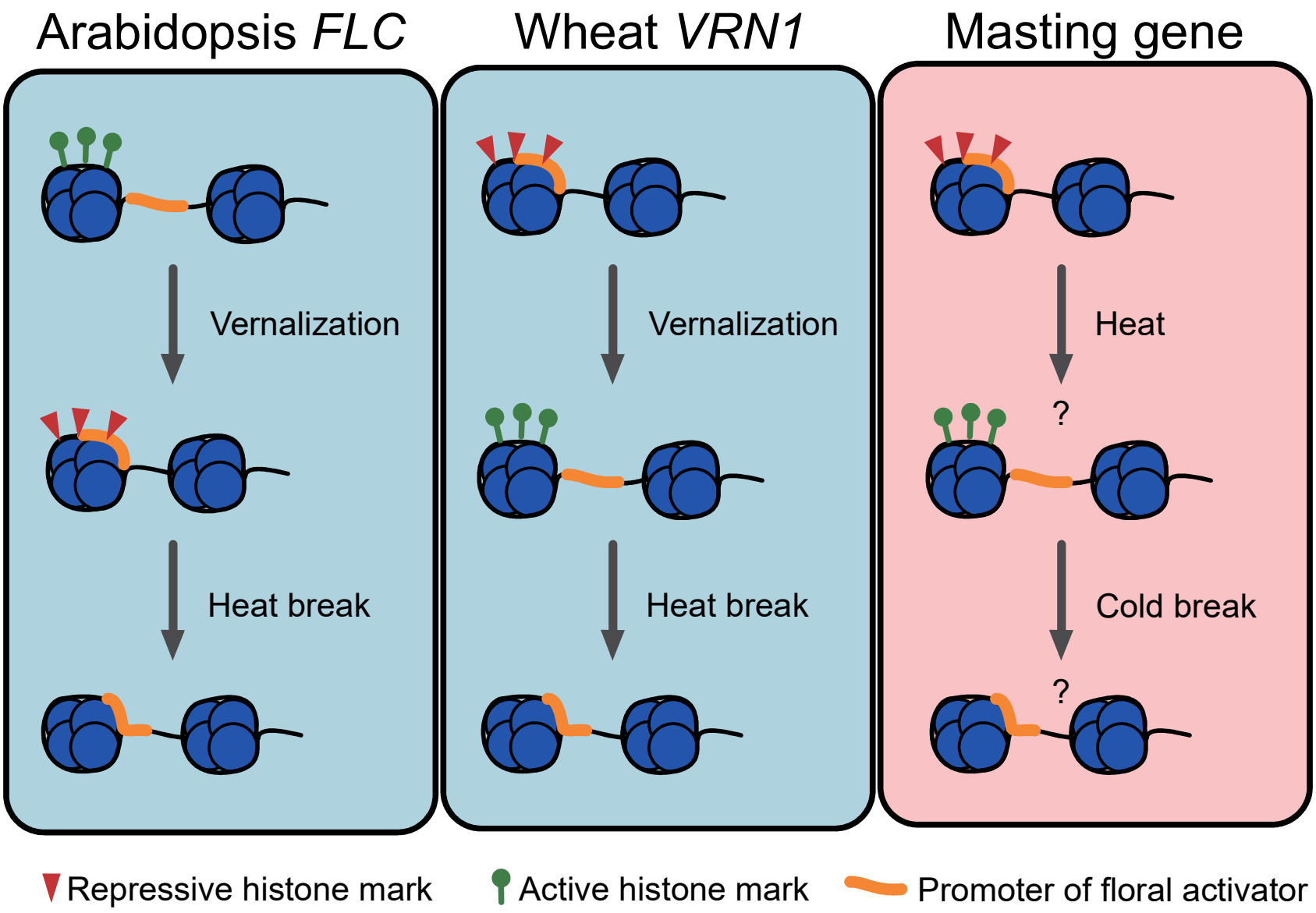
Arabidopsis *FLC*
Wheat *VRN1*
Masting gene
Vernalization
Vernalization
Heat
?
Heat break
Heat break
Cold break
?
Repressive histone mark
Active histone mark
Promoter of floral activator

Fig. 3

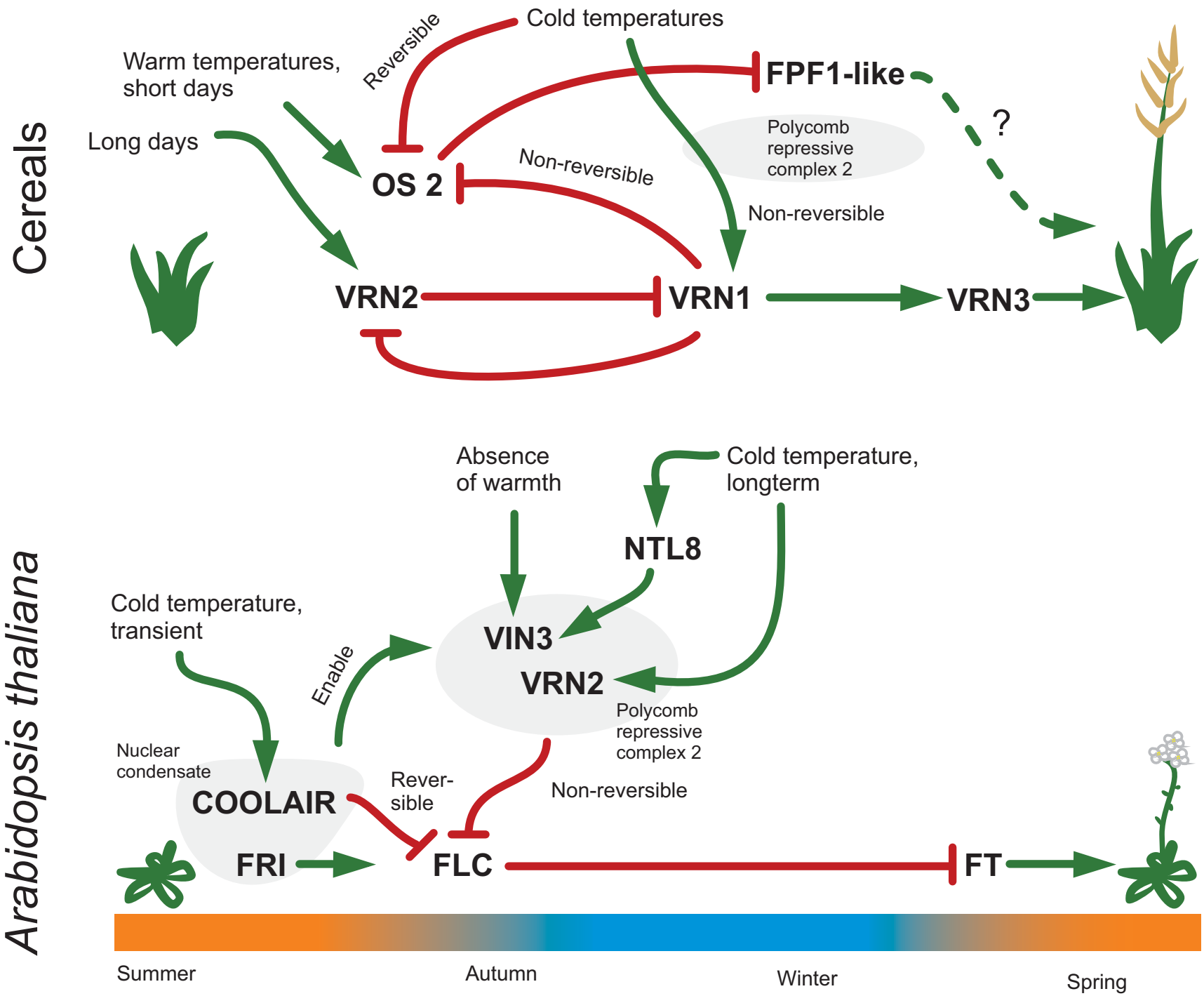
Cereals
Warm temperatures,
short days
Long days
Reversible
Cold temperatures
FPF1-like
?
Polycomb
repressive
complex 2
OS 2
Non-reversible
Non-reversible
VRN2
VRN1
VRN3
Arabidopsis thaliana
Absence
of warmth
Cold temperature,
longterm
NTL8
Cold temperature,
transient
Enable
VIN3
VRN2
Polycomb
repressive
complex 2
Nuclear
condensate
COOLAIR
Rever-
sible
Non-reversible
FRI
FLC
FT
Summer
Autumn
Winter
Spring

Fig. 4

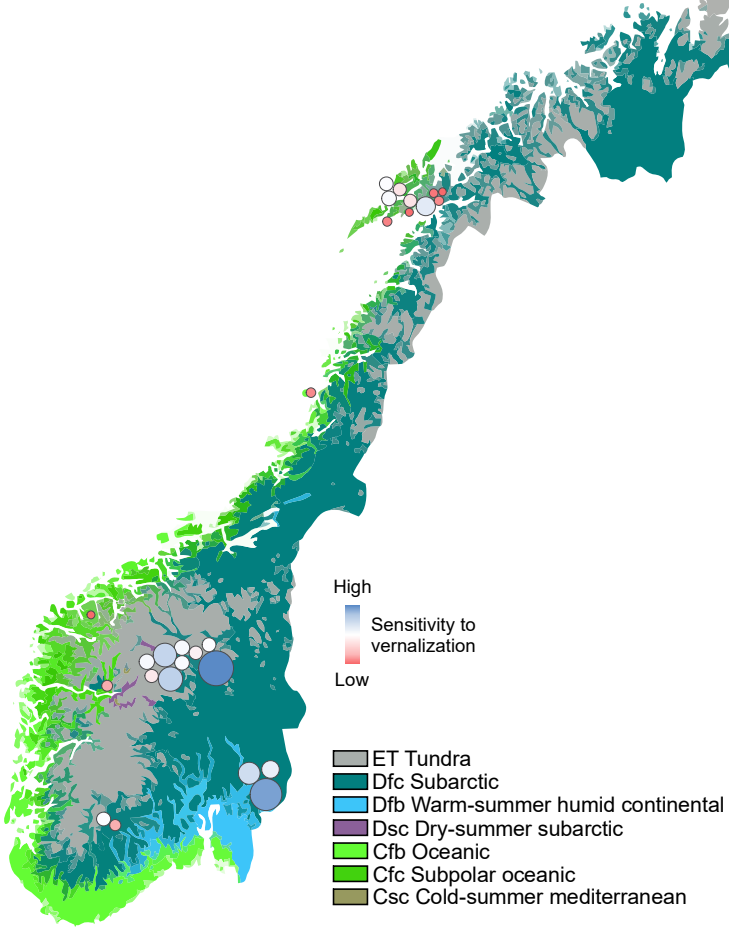
High
Sensitivity to vernalization
Low
ET Tundra
Dfc Subarctic
Dfb Warm-summer humid continental
Dsc Dry-summer subarctic
Cfb Oceanic
Cfc Subpolar oceanic
Csc Cold-summer mediterranean

Fig. 5