

REVIEW

Molecular genetic regulation of the vegetative–generative transition in wheat from an environmental perspective

Tibor Kiss^{1,2,*}, Ádám D. Horváth¹, András Cseh¹, Zita Berki¹, Krisztina Balla¹ and Ildikó Karsai^{1,*}

¹HUN-REN Centre for Agricultural Research, Agricultural Institute, H-2462 Martonvásár, Hungary, and ²Food and Wine Research Institute, Eszterházy Károly Catholic University, H-3300 Eger, Hungary

*For correspondence. E-mail kiss.tibor@atk.hu or karsai.ildiko@atk.hu

Received: 29 May 2024 Returned for revision: 8 September 2024 Editorial decision: 23 September 2024 Accepted: 30 September 2024

The key to the wide geographical distribution of wheat is its high adaptability. One of the most commonly used methods for studying adaptation is investigation of the transition between the vegetative–generative phase and the subsequent intensive stem elongation process. These processes are determined largely by changes in ambient temperature, the diurnal and annual periodicity of daylength, and the composition of the light spectrum. Many genes are involved in the perception of external environmental signals, forming a complex network of interconnections that are then integrated by a few integrator genes. This hierarchical cascade system ensures the precise occurrence of the developmental stages that enable maximum productivity. This review presents the interrelationship of molecular–genetic pathways (*Earliness per se*, circadian/photoperiod length, vernalization – cold requirement, phytohormonal – gibberellic acid, light perception, ambient temperature perception and ageing – miRNA) responsible for environmental adaptation in wheat. Detailed molecular genetic mapping of wheat adaptability will allow breeders to incorporate new alleles that will create varieties best adapted to local environmental conditions.

Key words: Adaptation, ageing, ambient temperature, circadian clock, earliness, gibberellin response, heading, light perception, photoperiod, vernalization, wheat.

INTRODUCTION

Wheat is the third most important cereal crop worldwide, and is an essential source of human food and animal feed (Shewry and Hey, 2015). Its production range (67°N to 45°S, Feldman, 1995) is characterized by wide macro- and microclimatic variation, to which plants can only adapt through wide genetic diversity (Cockram *et al.*, 2007; Distelfeld and Dubcovsky, 2010; Dreisigacker *et al.*, 2021). One of the most commonly used methods to investigate adaptation is the study of the transition between the vegetative–generative phase and the subsequent intensive stem elongation process. These processes are determined largely by changes in ambient temperature, the diurnal and annual periodicity of the photoperiod, and the composition of the light spectrum (Bullrich *et al.*, 2002; Lewis *et al.*, 2008; Hemming *et al.*, 2012; Karsai *et al.*, 2013; Kiss *et al.*, 2017; Dixon *et al.*, 2019; Monteagudo *et al.*, 2020). In temperate cereals, photoperiod and low-temperature vernalization are the two most decisive environmental factors determining the developmental processes of the plant (Cockram *et al.*, 2007; Distelfeld *et al.*, 2009a). In addition, several other factors fine-tune heading or flowering, including the ambient temperature above vernalizing levels and the various characteristics of light. Temperature has a more complex effect than photoperiod on the dynamics of plant development, as it can vary significantly not only seasonally, but also yearly and daily (Bullrich *et al.*, 2002; Lewis

et al., 2008; Hemming *et al.*, 2012). Therefore (in addition to its role in regulating the vernalization requirement), temperature significantly affects the heading (used synonymously with flowering) of cereals, the initiation rate, and number of leaves, tillers and spikelets (Slafer and Rawson, 1994; Atkinson and Porter, 1996; Slafer *et al.*, 2015). The spectral composition and intensity of light play an important role in the production of both primary and secondary metabolites through photosynthesis. Furthermore, they impact the determination of several developmental parameters, such as flowering time, growing process and the regulation of leaf initiation rate (Chen *et al.*, 2004; Darko *et al.*, 2014). However, only limited information is available on the relationship between light spectra variation and the complex genetic regulatory mechanism, including the role of circadian rhythm that determines the intensive stem elongation of hexaploid wheat. Results from experiments on barley confirmed that ambient temperature and spectral composition of light strongly modify plant development, even under fully inductive environmental conditions (saturated vernalization requirement and long-day illumination), which are otherwise optimal for differentiation of the floral meristem (Karsai *et al.*, 2013). Furthermore, while the genotypic effect of ambient temperature depends on the allelic distribution of the major developmental genes, this correlation was not confirmed for the spectral composition of light (Karsai *et al.*, 2013; Monteagudo *et al.*, 2020; Del Río *et al.*, 2023). A similar response to ambient

temperature has been described for wheat (Kiss *et al.*, 2017; Dixon *et al.*, 2019).

The molecular genetic regulation of plant development and the transition between the vegetative and generative phases in the dicotyledonous model plant *Arabidopsis thaliana* and in the monocotyledonous genera *Oryza*, *Brachypodium* and *Hordeum* have been studied most extensively (Schaffer *et al.*, 1998; Fowler *et al.*, 1999; Covington *et al.*, 2001; Izawa *et al.*, 2002; Yu *et al.*, 2002; Karsai *et al.*, 2005; Turner *et al.*, 2005; Yoo *et al.*, 2005; Cockram *et al.*, 2007; Higgins *et al.*, 2010; Campoli *et al.*, 2012a, 2012b, 2013; Cao *et al.*, 2020; Andrade *et al.*, 2022). Several known regulatory pathways exist with numerous interconnection points (Levy and Dean, 1998; Mouradov *et al.*, 2002; Komeda, 2004; Kim *et al.*, 2009; Fornara *et al.*, 2010). These pathways include circadian/photoperiod, vernalization (the effect of low temperature), ambient temperature, phytohormones [gibberellic acid (GA)], earliness per se and ageing regulation [micro-RNA (miRNA)]. The signals from the different regulatory elements are collected by a few integrator genes and transmitted to the floral meristem identity genes, which are responsible for the generative transition of the apex and the regular development of the different floral organs, respectively. The molecular genetic process of the developmental phase in wheat is much less well understood, and only the major components of the vernalization and photoperiod regulation pathways have been identified in detail (Worland, 1996; Dubcovsky *et al.*, 1998; Worland *et al.*, 1998), using either the diploid *Triticum monococcum* and tetraploid species with a smaller genome size or specific crossing lines (RIL – recombinant inbred line, NIL – near-isogenic line, mutant and transgenic lines) (Trevaskis *et al.*, 2003; Loukoianov *et al.*, 2005; Dubcovsky *et al.*, 2006; Yan *et al.*, 2006; Shimada *et al.*, 2009; Distelfeld and Dubcovsky, 2010; Li *et al.*, 2011; Chen and Dubcovsky, 2012; Kumar *et al.*, 2012; Kippes *et al.*, 2016). Results have revealed significant differences between the regulatory genes and regulatory mechanisms of *Arabidopsis* and cereals, which is particularly striking in the case of vernalization regulation. The genetic regulation of wheat circadian rhythm and GA synthesis is also not well understood, as vernalization and photoperiod responses can mask their effects, making them extremely difficult to study. Also, little information is available on the extent of variability in the phenotypic effects of different alleles as related to heading under field conditions due to the complex interaction of various environmental factors in different years (Kiss *et al.*, 2019; Horváth *et al.*, 2023). There is also a basic difference, however, between *Arabidopsis* and cereals from aspects of both the generative development of inflorescences and intensive stem elongation (Fig. 1). In *Arabidopsis*, these processes occur in parallel, but in cereals they are separated in time: the generative development of inflorescences is already at advanced stages by the time intensive stem elongation actually starts (Kiss *et al.*, 2017; Monteagudo *et al.*, 2020).

In summary, genetic regulatory mechanisms that evolved in response to abiotic environmental (vernalization temperature, photoperiod, ambient temperature, light intensity and composition) factors ensure that flowering and ripening occur under optimal environmental conditions. Detailed molecular genetic analysis of wheat heading time may become even more valuable in the future, as rapidly and unpredictably changing

macro- and microclimatic influences will increase the need for breeders to find genetic materials in different breeding programmes to produce new varieties that are best adapted to local environmental conditions. This review focuses on the main molecular–genetic regulatory mechanisms responsible for adaptation in wheat (Fig. 2; Table 1).

THE MAIN GENETIC DETERMINANTS OF TIME TO HEADING

Vernalization pathway

Temperate cereals have various mechanisms that can protect the floral meristem from the adverse effects of low temperatures and allow for heading after saturation of the cold requirement (Cockram *et al.*, 2007; Brambilla *et al.*, 2017; Fernández-Calleja *et al.*, 2021). During breeding, mutations in the genes involved in determining vernalization requirement (VERNALIZATION – VRN) have produced different developmental types of cereal varieties (winter, spring and facultative) with different requirements for low temperatures. Winter types require a longer vernalization period for optimal flowering (Trevaskis, 2010). In wheat, several gene families are involved in the genetic regulation of the vernalization requirement, of which VRN1 (on the homologous group of chromosome 5), VRN2 (on 4B, and on the telomeric region of 5A) and VRN3 (on the homologous group of chromosome 7) have major regulatory roles (Law *et al.*, 1976; Snape *et al.*, 2001; Barrett *et al.*, 2002; Iwaki *et al.*, 2002; Galiba *et al.*, 2009; Distelfeld and Dubcovsky, 2010). However, the data do not provide a detailed understanding of the environmentally determined interconnections between these gene families in regulating the later developmental phases including the process of stem elongation, beyond their roles in the vegetative–generative transition (Trevaskis *et al.*, 2007a; Distelfeld *et al.*, 2009b; Shimada *et al.*, 2009; Distelfeld and Dubcovsky, 2010). In barley, different allele combinations of genes that are responsible for the regulation of vernalization requirement and photoperiod sensitivity lead to different plant development types (Karsai *et al.*, 2008).

The VRN1 gene in wheat encodes an important transcription factor of the MINICHROMOSOME MAINTENANCE1/AGAMOUS/DEFICIENS/SERUM RESPONSE FACTOR (MIKC) family of MADS-box genes, which most closely resembles the APETALA1/FRUITFULL class of *Arabidopsis* MADS-box genes (API/FUL) (Yan *et al.*, 2003; Hyles *et al.*, 2020). These genes are important for regulating the transition from the vegetative shoot apex to the generative phase (Mandel and Yanofsky, 1995; Ferrándiz *et al.*, 2000; Shitsukawa *et al.*, 2007b). In contrast to *Arabidopsis* API/FUL genes, the expression of VRN1 in wheat is increased by prolonged exposure to cold (Danyluk *et al.*, 2003; Murai *et al.*, 2003; Trevaskis *et al.*, 2003; Yan *et al.*, 2003). However, the precise mechanism of the low-temperature induction of VRN1 is not yet understood, but various modifications of histone proteins (H3K27 and H3K4 – DNA methylation) are presumed to play a prominent role. These protein modifications both maintain the repressed state of VRN1 before winter and also induce increased transcription of this gene after the cold requirement (Diallo *et al.*, 2012; Yuan *et al.*, 2013; Hyles *et al.*, 2020; Chen *et al.*, 2023).

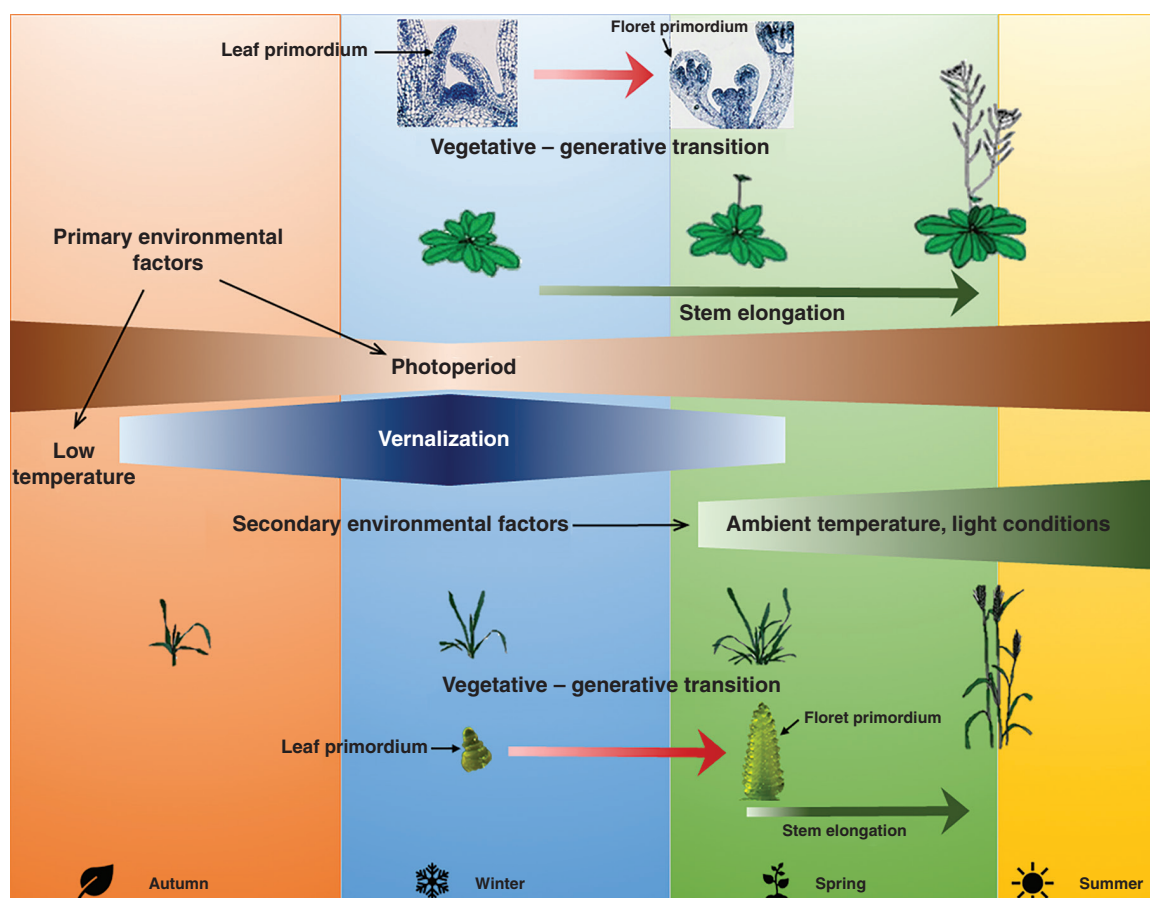


FIGURE 1. Differences between the generative development of inflorescences and the rate of intensive stem elongation in *Arabidopsis* versus cereals. In *Arabidopsis* these processes occur mostly in parallel, but in cereals they are separated in time; the generative development of the inflorescences is already at advanced stages by the time intensive stem elongation actually starts (Kiss *et al.*, 2017; Monteagudo *et al.*, 2020).

Oliver *et al.* (2009) found a correlation between histone protein levels and *VRN1* activity. Active histone proteins may be derived from cell organization and may also play a role in cellular ‘vernalization’ memory (Distelfeld *et al.*, 2009a; Oliver *et al.*, 2009; Chen and Dubcovsky, 2012). Transcription of *VRN1* is significantly higher in vernalized plants under short photoperiod than in plants without cold treatment (Dubcovsky *et al.*, 2006; Trevaskis *et al.*, 2006; Fu *et al.*, 2007); therefore, *VRN1* genes are upregulated by vernalization, independently of the function of the other two important *VRN* genes (*VRN2*, *VRN3*) (Trevaskis *et al.*, 2007a). Similar to *VRN1*, the *WHEAT VEGETATIVE TO REPRODUCTIVE TRANSITION-1* (*TaVRT-1*) and *WHEAT APETALA1* (*WAP1*) genes encode an *APETALA1* (*API*)-like MADS-box gene (presumably *VRN1* orthologues). They also play a major role in the vegetative–generative transition of wheat, but they are not sufficient either by themselves or in combination to induce heading (Danyluk *et al.*, 2003; Murai *et al.*, 2003; Trevaskis *et al.*, 2003; Yan *et al.*, 2003). Subsequent studies have shown that these two genes are synonymous with *VRN1* (Kane *et al.*, 2007; Shitsukawa *et al.*, 2007a). A number of functional polymorphisms have been found in the promoter, exon and intron regions of *VRN-A1*, including gene copy number variations (Yan *et al.*, 2004a; Fu *et al.*, 2005; Dubcovsky *et al.*, 2006; Golovkina *et al.*, 2010;

Kamran *et al.*, 2014; Shcherban *et al.*, 2015, 2016; Ivaničová *et al.*, 2016; Muterko *et al.*, 2016; Muterko and Salina, 2017; Steinfert *et al.*, 2017; Strejčková *et al.*, 2021; Milec *et al.*, 2023; B. Zhang *et al.*, 2023). The basic allele type of spring/winter is associated with sequence differences detected in several promoter regions, and a larger insertion/deletion size identified in the intron 1 region (Yan *et al.*, 2004a; Fu *et al.*, 2005). For the other two *VRN1* genes (*VRN-B1* and *VRN-D1*), much less polymorphism was detected, and the spring–winter allele type is basically related to insertion/deletion of the intron 1 region (Yan *et al.*, 2004a; Fu *et al.*, 2005; Santra *et al.*, 2009; Golovkina *et al.*, 2010; Chu *et al.*, 2011; Efremova *et al.*, 2011; Milec *et al.*, 2012, 2013, 2023; Shcherban *et al.*, 2012; J. Zhang *et al.*, 2012; Kamran *et al.*, 2014; Muterko *et al.*, 2015; B. Zhang *et al.*, 2018; Strejčková *et al.*, 2021; Makhoul *et al.*, 2022). Copy number variation (CNV) has also been found in the *VRN1* genes, which is particularly significant for *VRN-A1* (Fu *et al.*, 2005; Díaz *et al.*, 2012; Kippes *et al.*, 2015; Würschum *et al.*, 2015; Muterko and Salina, 2019, 2021; Strejčková *et al.*, 2021). The strength of the correlation between *VRN-A1* copy number and heading time is strongly influenced by the developmental type of each copy. Thus, wheat genotypes that contain more copies of the winter type allele have a much higher vernalization requirement, and they tend to have later heading

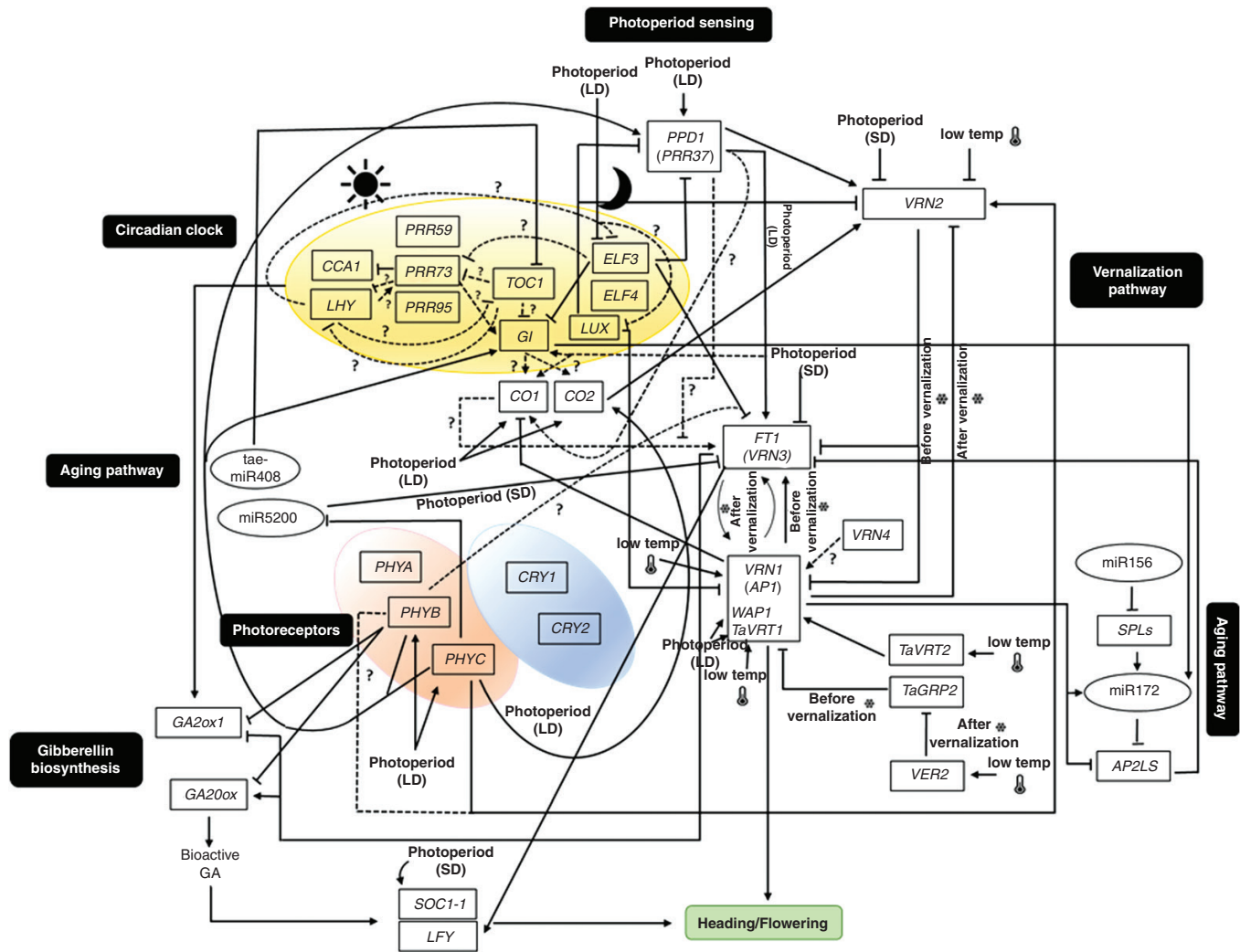
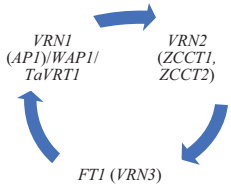


FIGURE 2. Regulatory relationships of major flowering genes in wheat. Boxes represent genes, while ellipses indicate other genetic factors. Arrows indicate the promotion of gene expression; lines with blunt ends show repression of gene expression. Dotted lines designate probable interactions of the genes presented on the basis of data on interactions of appropriate *Arabidopsis* genes. *Arabidopsis* orthologues of some key flowering genes in wheat are shown in parentheses. LD: long-day illumination, SD: short-day illumination, temp: temperature. The visualized gene regulatory network has been extended based on Cockram *et al.* (2007), Trevaskis *et al.* (2007b), Distelfeld *et al.* (2009a), Chen and Dubcovsky (2012), Fjellheim *et al.* (2014), Kiseleva and Salina (2018), Cao *et al.* (2021), Debernardi *et al.* (2022) and Li *et al.* (2024). Abbreviations: AP2L, APETALA2-like; CCA1, CIRCADIAN CLOCK-ASSOCIATED 1; CO1, CONSTANS 1; CO2, CONSTANS 2; CRY1, CRYPTOCHROME 1; CRY2, CRYPTOCHROME 2; ELF3, EARLY FLOWERING 3; ELF4, EARLY FLOWERING 4; GA, gibberellic acid; GA20ox, GA20 oxidase; GA2ox1, GA2 oxidase 1; G1, GIGANTEA; LFY, LEAFY; LHY, LATE-ELONGATED HYPOCOTYL; LUX, ARRHYTHMO; miR156, microRNA156; miR172, microRNA172; miR5200, microRNA5200; PHYA, PHYTOCHROME A; PHYB, PHYTOCHROME B; PHYC, PHYTOCHROME C; PPD1, PHOTOPERIOD1; PRR59, PSEUDORESPONSE REGULATOR 59; PRR73, PSEUDORESPONSE REGULATOR 73; PRR95, PSEUDORESPONSE REGULATOR 95; SOC1-1, SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1-1; SPL, SQUAMOSA PROMOTER BINDING LIKE; ta-miR408, *T. aestivum*-microRNA408; TaGRP2, *T. aestivum* glycine-rich RNA binding protein 2; TaVRT1, Wheat vegetative to reproductive transition-1; TaVRT2, Wheat vegetative to reproductive transition-1; TOC1, TIMING OF CAB EXPRESSION1; VER2, vernalization-related 2; VRN1, VERNALIZATION1 (APETALA1); VRN2, VERNALIZATION2; FLOWERING LOCUS T1 (FT1), VRN3 (VERNALIZATION3); VRN4, VERNALIZATION4; WAP1, Wheat APETALA1.

(Würschum *et al.*, 2015; Muterko and Salina, 2019, 2021; Strejčková *et al.*, 2021; Chen *et al.*, 2024). In relation to the transcriptional expression of *VRN1* genes, Loukoianov *et al.* (2005) found that the three *VRN1* genes (*VRN-A1*, *VRN-B1* and *VRN-D1*) showed different expression levels in isogenic wheat lines between the one- and six-leaf developmental stages. The transcription of *VRN-A1* was already expressed in the first leaf stage, whereas the activity of *VRN-B1* and *VRN-D1* alleles was only detectable in the second and third leaf stages, which may explain its stronger impact on regulation (Loukoianov *et al.*,

2005). This phenomenon was confirmed to be the result of the different attributes of dominant/recessive allele types associated with the distinct mutations in each subgenome (promoter insertion in genome A, intron deletions of different lengths in genomes B and D) (Trevaskis *et al.*, 2003; Kippes *et al.*, 2018; Hyles *et al.*, 2020). It was also established that *VRN1* expression follows a diurnal pattern, but little information is available on its variability across genotypes or on its dependence on various environmental factors and whether these variations may have any phenotypic consequences (Shimada *et al.*, 2009;

TABLE 1. Reference list of major genetic regulation networks connected to flowering time in wheat (as a complement to Fig. 2).

Pathways of molecular genetic regulation of plant development	Interaction of genes and other genetic factors	Reference(s)
Vernalization	 VRN1 (API)/WAP1/TaVRT1 VRN2 (ZCCT1, ZCCT2) FT1 (VRN3) VRN1 → SOC1-1, LFY VRN4 → VRN1 (API) VER2 → TaGRP2 TaGRP2 → VRN1 (API) TaVRT2 → VRN1 (API)	Danyluk <i>et al.</i>, 2003; Murai <i>et al.</i>, 2003; Trevaskis <i>et al.</i>, 2003, 2006, 2007a, 2007b; Dubcovsky <i>et al.</i>, 2006; Yan <i>et al.</i>, 2003, 2004a, 2004b, 2006; Cockram <i>et al.</i>, 2007; Kane <i>et al.</i>, 2007; Shitsukawa <i>et al.</i>, 2007a; Hemming <i>et al.</i>, 2008; Distelfeld <i>et al.</i>, 2009b; Trevaskis, 2010; Chen and Dubcovsky, 2012; Fjellheim <i>et al.</i>, 2014; Kiseleva and Salina, 2018; Cao <i>et al.</i>, 2021; Debernardi <i>et al.</i>, 2022 Pearce <i>et al.</i>, 2013 Kippes <i>et al.</i>, 2014; Hyles <i>et al.</i>, 2020 Yong <i>et al.</i>, 2003; Xing <i>et al.</i>, 2009; Xiao <i>et al.</i>, 2014 Xiao <i>et al.</i>, 2014 Xie <i>et al.</i>, 2021
Photoperiod	PPD1 (PRR37) → VRN2 (ZCCT1, ZCCT2), FT1 (VRN3), CO1	Yan <i>et al.</i> , 2006; Beales <i>et al.</i> , 2007; Díaz <i>et al.</i> , 2012; Shaw <i>et al.</i> , 2012, 2020; Hyles <i>et al.</i> , 2020; Shaw <i>et al.</i> , 2020
Circadian clock	CCA1 → PRR73	Kiseleva and Salina, 2018
	LHY → PRR73, ELF3, LUX	Kiseleva and Salina, 2018
	TOC1 → PRR73, LHY, GI	Kiseleva and Salina, 2018
	GI → CO1/CO2, VRN2 (ZCCT1, ZCCT2), FT1 (VRN3)	Zhao <i>et al.</i> , 2005; Li <i>et al.</i> , 2024
	CO1/CO2 → FT1 (VRN3)	Campoli <i>et al.</i> , 2012a; Alqudah <i>et al.</i> , 2014; Johansson and Staiger, 2014; Mulki and von Korff, 2016; Shaw <i>et al.</i> , 2020
	LUX → PPD1 (PRR37), VRN1 (API), VRN2 (ZCCT1, ZCCT2)	Mizuno <i>et al.</i> , 2016; Nishiura <i>et al.</i> , 2018
	ELF3/ELF4 → PPD1 (PRR37), GI	Yu <i>et al.</i> , 2008; Alvarez <i>et al.</i> , 2016, 2023; Zikhali <i>et al.</i> , 2016
Light perception	PHYB, PHYC → PPD1 (PRR37), VRN2 (ZCCT1, ZCCT2)	Chen <i>et al.</i> , 2014; Pearce <i>et al.</i> , 2016; Kiseleva and Salina, 2018
Gibberellin response	GA20ox → FT1 (VRN3)	Pearce <i>et al.</i> , 2013
	GA2ox1 → FT1 (VRN3)	
Ageing	tae-miR408 → TOC1	Zhao <i>et al.</i> , 2016b
	miR5200 → PHYC, FT1 (VRN3)	Wu <i>et al.</i> , 2013; Pearce <i>et al.</i> , 2016
	miR156 → SPLs	Debernardi <i>et al.</i> , 2022
	miR172 → AP2Ls, VRN1 (API), GI	Wu <i>et al.</i> , 2009; Debernardi <i>et al.</i> , 2022; Li <i>et al.</i> , 2024
	AP2Ls → VRN1 (API), FT1 (VRN3)	Debernardi <i>et al.</i> , 2022

Nishiura *et al.*, 2014, 2018). The dominant *Vrn-A1* allele also determines the spring type that requires no cold treatment at all for heading. In contrast, the dominant *Vrn-B1*, *Vrn-D1* and *Vrn4* genes only partially abolish the cold requirement that is essential for the generative phase (Pugsley, 1971, 1972; Kato *et al.*, 2001; Loukoianov *et al.*, 2005).

Two similar ‘zinc-finger CCT’ genes (*ZCCT1* and *ZCCT2*) have been identified in the *VRN2* locus which are involved in dominant flowering-inhibitory mechanisms (Yan *et al.*, 2004b). No *VRN2* orthologue gene has yet been found either in rice or in *Arabidopsis*, so it appears that this gene is a distinct regulatory element appearing during the evolution of cereals (Yan *et al.*, 2004b). During vernalization, a steady decrease in the

levels of transcription factors produced by *ZCCT1* and *ZCCT2* was detected in the leaves, while the activity of *ZCCT* genes remained high in winter types that were kept at room temperature as controls (Yan *et al.*, 2004b). Short photoperiod inhibits, while long day stimulates *VRN2* expression (Dubcovsky *et al.*, 2006; Trevaskis *et al.*, 2006). In barley, both phenomic and gene expression analyses have confirmed that *VRN2* appears to be controlled by both *CONSTANS* (*CO*) and *VRN1*, suggesting that this gene is a joint element in photoperiod and vernalization regulatory pathways (Karsai *et al.*, 2005, 2006; Mulki and von Korff, 2016). In hexaploid wheat, the phenotypic effects of loss-of-function alleles of *VRN2* are extremely difficult to study because the redundancy across the subgenomes may hide

the effect of a single recessive allele. However, the induction of new allelic variants of this gene (Dubcovsky and Dvorak, 2007; Distelfeld *et al.*, 2009b; Tan and Yan, 2016; Milec *et al.*, 2023) may also broaden the adaptive capacity of wheat (through increased genetic diversity) (Hyles *et al.*, 2020). Tan and Yan (2016) reported the duplication of the *VRN-B2* gene in hexaploid wheat, but they found no significant effect on flowering time.

Wheat *FLOWERING LOCUS T* (*TaFT1*), identified as *VRN3*, encodes a RAF kinase inhibitor protein (highly similar to the *FT* gene of *Arabidopsis*) that functions as a signal transduction molecule (an integrator of vernalization and photoperiod regulatory pathways) and, as such, it is an essential element of flowering (Yan *et al.*, 2006; Shi *et al.*, 2019). At least 12 *FT*-like genetic regions have currently been identified in bread wheat and barley (Lv *et al.*, 2014; Bennett and Dixon, 2021; Pieper *et al.*, 2021), of which *Vrn-B3* is the most well characterized; the dominant allele was found to have a 5295-bp repetitive sequence insertion in the promoter region, which showed a strong correlation with early flowering. The recessive (*vrn-B3*) allele of this gene with the deletion caused late heading (Yan *et al.*, 2006). Moreover, Finnegan *et al.* (2018) described that the late heading observed in relation to deletion was associated with a prolonged spikelet initiation phase, which increased the number of spikelets during long days. Shaw *et al.* (2019) reported a weak interaction between *TaFT2* and heading as well as a stronger association with spikelet number in tetraploid wheat. Gauley and Boden (2021) also observed a strong correlation between *FT2* and *PPD1* gene expression and regulation of spikelet number in hexaploid wheat. Gene expression studies revealed that *FT3* orthologous genes of tetra- and hexaploid wheat were upregulated only under short photoperiod, similar to the expression of *HvFT3* (Halliwell *et al.*, 2016). Six additional single nucleotide polymorphisms (SNPs) were found in the promoter and intron 1 regions, but these mutations did not cause phenotypic differences between the two main allele types (Yan *et al.*, 2006). Chen *et al.* (2013) and Berezhnaya *et al.* (2021) identified two additional allele types at the *VRN3* locus (*VRN-B3b*, *VRN-B3c* and *VRN-B3d*, *VRN-B3e*). Other polymorphisms linked to *VRN3* have also been reported (Bonnin *et al.*, 2008; Zikhali *et al.*, 2017; Chen *et al.*, 2020a; Dreisigacker *et al.*, 2021; Nishimura *et al.*, 2021), but copy number differences have so far only been detected in barley (Nitcher *et al.*, 2013; Milec *et al.*, 2023). There is a difference in *VRN3* signalling between *Arabidopsis* and wheat. While *FT* in *Arabidopsis* directly transmits the signal to the floral meristem identity genes via *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1* (*SOC1*), in wheat, *VRN3* is transmitted via *VRN1* expressed in the apical meristem. Luo *et al.* (2024) demonstrated a repressor role for the wheat *SOC1* gene in the vernalization and photoperiod regulatory pathway. Kiss *et al.* (2017) showed that, with the exception of *VRN3*, ambient temperature also has a significant effect on the expression of the main developmental genes (*VRN1*, *VRN2* and *PPD1*), the extent of which can be significantly influenced by daylength.

Little information is available on *VRN4*, and some authors suggest that the dominant allele of *VRN-D4* has a low distribution among hexaploid wheat genotypes (Goncharov, 1998, 2003). The extra *VRN1* gene copy present at the *VRN4* locus (as

a probable result of translocation) may be associated with elevated transcription levels of *VRN1*, which reduces the need for vernalization (Kippes *et al.*, 2014). The intron polymorphisms (SNPs) observed in this translocation explain the high expression of *VRN1* in genotypes that carry *VRN4* (Hyles *et al.*, 2020). As with other *VRN* genes, *VRN-D4* encodes an AP1 protein that shares a high degree of similarity with the *Arabidopsis* meristem identity protein AP1 (Shi *et al.*, 2019). Kippes *et al.* (2015) described the Australian origin of *VRN4*, which can be traced back to the ‘Gabo’ variety and has a significant role in adapting to local environmental conditions through its strong spring growing habit (Hyles *et al.*, 2020). In wheat, phenotypic values and gene expression patterns have shown that there is a close epistatic interaction between *VRN1*, *VRN2* and *VRN3* making it difficult to clearly identify the primary target gene in the vernalization process (Distelfeld and Dubcovsky, 2010). However, *VRN1* appears to play a key role (Danyluk *et al.*, 2003; Trevaskis *et al.*, 2003; Yan *et al.*, 2003; Shitsukawa *et al.*, 2007b).

Other vernalization-induced genes have also been described in wheat, such as *Vernalization-related 2* (*VER2*), *Wheat vegetative to reproductive transition-2* (*TaVRT-2*) and *T. aestivum* *glycine-rich RNA binding protein 2* (*TaGRP2*) (Chong *et al.*, 1998; Yong *et al.*, 2003; Kane *et al.*, 2005; Xing *et al.*, 2009; Xiao *et al.*, 2014). Prior to vernalization, the protein produced by *TaGRP2* binds to a specific region of *VRN1* and represses the accumulation of its transcript. However, after vernalization, *VER2* expression is increased, and the phosphorylated *VER2* protein coupled with *TaGRP2* protein resolves its inhibitory effect on *VRN1* (Xiao *et al.*, 2014). Previous studies have found that the regulation of *TaVRT2* is independent of vernalization and photoperiod sensing pathways and that its gene product accumulates in the vegetative phase, which can be directly linked to the CArG box part of the promoter region of *VRN1* inhibiting the activity of this gene. This effect is further enhanced by *VRN2*. After vernalization, the expression of both genes is inhibited, triggering an increase in *VRN1* activity (Kane *et al.*, 2005, 2007). However, a series of subsequent studies showed that the expression of *TaVRT2* and *HvVRT2* (orthologous gene in barley) genes was induced by vernalization (Trevaskis *et al.*, 2007a; Dubcovsky *et al.*, 2008; Winfield *et al.*, 2009; Li *et al.*, 2018); thus, they are promoters of the vernalization regulatory pathway together with *TaVRN1* (Xie *et al.*, 2021). *TaVRT2* expression increases steadily during vernalization and then decreases significantly, which may prevent the detection of its significant effect on flowering (Xie *et al.*, 2021).

Based on recent models of the vernalization regulation pathway (Chen and Dubcovsky, 2012; Debernardi *et al.*, 2022; Li *et al.*, 2024), in autumn, after germination, when the days are still sufficiently long, the active *VRN2* prevents transcription of *VRN3*, which may play an important role in keeping *VRN1* activity low (Trevaskis *et al.*, 2006; Hemming *et al.*, 2008). During vernalization, *VRN1* is progressively activated by cold. The increasing amounts of the *VRN1* transcription factor inhibit the function of *VRN2* (its protein is directly linked to the promoter region of *VRN2*) and, in parallel, they stimulate *VRN3* (its protein is directly linked to the promoter region of *VRN3*). *VRN3* protein thus activated is transported via the phloem to the meristematic tissue of the shoot apex (Trevaskis *et al.*,

2006; Distelfeld *et al.*, 2009a; Deng *et al.*, 2015). The increased amount of *VRN3* further enhances the activity of *VRN1* and induces heading (Kardailsky *et al.*, 1999; Kobayashi *et al.*, 1999; Abe *et al.*, 2005; Loukoianov *et al.*, 2005; Preston and Kellogg, 2008; Distelfeld and Dubcovsky, 2010; Chen and Dubcovsky, 2012; Fjellheim *et al.*, 2014; Johansson and Staiger, 2014; Deng *et al.*, 2015) (Fig. 2; Table 1). The flowering regulation model reported by Debernardi *et al.* (2022) was complemented with an ageing regulation pathway. Based on the results of Shaw *et al.* (2020), the model can be further extended by the finding that, in autumn, *PPD1*, *CO1* and *CO2* genes promote the expression of *VRN2*, and after vernalization, the activated *VRN1* downregulates *VRN2* and *CO1*, promoting the expression of *FT1*, a process that is further enhanced by the *PPD1* gene. In barley, the possible photoperiod-dependent relationship between *PPD-H1* and *VRN-H1* was confirmed by phenomic studies (Karsai *et al.*, 1997; Parrado *et al.*, 2023).

In summary, while there is a similarity in the genetic regulatory mechanism of the vernalization requirement in mono- and dicotyledonous plants (based on epigenetic histone modification of the promoter of the regulated gene), there is a large difference between the target genes. The main regulatory gene for these processes in *Arabidopsis* is *FLOWERING LOCUS C* (*FLC*), which acts as a repressor in the transduction of the floral meristem, whereas in wheat, it is *VRN1* demonstrating a central activator role (Sheldon *et al.*, 2000; Loukoianov *et al.*, 2005; Li and Dubcovsky, 2008).

Photoperiod sensitivity

To detect diurnal and seasonal changes in daylength, plants have had to develop different adaptive systems, in which the gene clusters responsible for photoperiod sensitivity (*PHOTOPERIOD1/PPD1*), genes regulating the internal circadian rhythm, and primary light-sensing molecules such as phytochromes (*PHY*) and cryptochromes (*CRY*) play an important role (Mizuno and Nakamichi, 2005; Hyles *et al.*, 2020). Plants can be divided – according to their photoperiod sensitivity – into long-day, short-day and so-called daylength-neutral classes (Garner and Allard, 1920). Long-day plants, such as wheat, barley, rye and *Arabidopsis*, need a long-day illumination to flower properly, otherwise their development will be stunted (Laurie, 1997). For short-day crops, such as maize and rice, a shorter daylight is sufficient for flowering (Laurie, 1997). In contrast to the genetic control of vernalization processes, the photoperiod regulatory pathway shows a higher level of similarity in both monocotyledonous and dicotyledonous plants, in which the activity of *FT* (*TaFT1* in wheat) has a central regulatory role under inductive illumination (Kardailsky *et al.*, 1999; Kobayashi *et al.*, 1999) and *CO1/CO2* can modulate its activity (Kitagawa *et al.*, 2012). In *Arabidopsis*, the wild-type dominant *CO* resulted in late flowering under short days and early flowering under long days. In contrast, in cereals, genotypes containing the recessive *co* caused late flowering under both daylengths (Laurie, 1997). For long-day plants, a so-called daylength-uninfluenced developmental phase has been described after germination, followed by a light-inducible phase (Roberts *et al.*, 1988). In the period not affected by light, plants do not sense or cannot

respond to different daylengths, so their heading time is not affected. The length of this phase may vary between genotypes. When plants enter the so-called light-inducible developmental phase, different daylengths already affect flowering time, but the response of individual genotypes can vary over a wide range (Roberts *et al.*, 1988). In wheat, the gene clusters responsible for the regulation of photoperiod sensitivity (*PPD1*) mainly determine flowering time, along with the *VRN* genes. The wild ancestors of wheat are quantitative long-day plants, which are capable of heading under short days, but this process is greatly accelerated by long illumination (Greenup *et al.*, 2009). However, mutations in *PPD1* genes (*PPD-A1*, 2A; *PPD-B1*, 2B; and *PPD-D1*, 2D) during breeding resulted in photoperiod-sensitive (*Ppd-1b* – recessive) and photoperiod-insensitive (*Ppd-1a* – semi-dominant) types (Pugsley, 1966; Law *et al.*, 1978; McIntosh *et al.*, 2003). In wheat and barley, *PPD1* plays a more important role in the regulation of flowering by photoperiod than *CO1* and *CO2* genes (Alqudah *et al.*, 2014; Shaw *et al.*, 2020). Several studies have shown that under both long- and short-day illumination, photoperiod-insensitive alleles shortened the time needed to heading (under both controlled and field conditions). However, the photoperiod-sensitive allele significantly delays this process in the short day (Worland *et al.*, 1998; Foulkes *et al.*, 2004; Jones *et al.*, 2017). There is evidence that the initial time and length of the stem elongation phase are also highly dependent on the effect of different alleles of the gene responsible for different photoperiod sensing (Miralles *et al.*, 2000; Horváth *et al.*, 2023). This developmental phase is critical to the formation of the total number of fertile florets, which is closely linked to grain yields (Fischer, 1985; Slafer and Rawson, 1994; Reynolds *et al.*, 2009; García *et al.*, 2011; Guo *et al.*, 2018).

PPD1 belongs to the pseudoresponse regulator (*PRR*) gene family, and is known as *PRR37* (Beales *et al.*, 2007). In addition, *PPD1* is closely related to the *Arabidopsis* *PRR7* gene which also plays a role in light and temperature sensing of the circadian rhythm, so *PPD1* may have a similar role in cereals (Beales *et al.*, 2007; Greenup *et al.*, 2009). Although the regulation of *TaPRR37* in wheat is also dependent on circadian genes, this gene is not part of the transcriptional/translational feedback loop that determines circadian rhythm (Kiseleva *et al.*, 2022). In terms of functional polymorphisms, the least information is available on *PPD-A1*; only a few polymorphisms have been described so far in photoperiod-insensitive varieties (Beales *et al.*, 2007; Wilhelm *et al.*, 2009; Nishida *et al.*, 2013b; Makhoul *et al.*, 2024). Breeders might also use the photoperiod-insensitive allele type *PPD-A1a* to fine-tune the photoperiod sensitivity of wheat at higher latitudes (Lin *et al.*, 2021). *PPD-B1* functional polymorphisms are better known than those of *PPD-A1*. It was found that the heading time in substitution lines carrying the single-chromosome photoperiod-insensitive allele 2B was shorter than that of the photoperiod-sensitive allele (Scarath and Law, 1984). In Chinese Spring variety, a point mutation in the exon 3 region has been described, and it has also been shown that a multiplication of the *PRR* gene copy number is behind the photoperiod insensitivity (Díaz *et al.*, 2012). These mutations show co-segregation with the early heading phenotype (Beales *et al.*, 2007; Díaz *et al.*, 2012; Würschum *et al.*, 2015, 2018). Cane *et al.* (2013), Langer *et al.* (2014) and Kiss *et al.* (2014b) in three multi-varietal wheat panels of distinctly diverse

geographical origins (Australian vs. mostly European) have independently demonstrated that there is a strong correlation between *PPD-B1* gene copy number variants and flowering time in a wide genetic pool under field conditions. *PPD-D1* in wheat, which shows similarity to *PPD-H1* in barley, has the strongest influence on photoperiod sensitivity (Laurie *et al.*, 1995; Börner *et al.*, 1998; Beales *et al.*, 2007), but there are significant differences between the two genes (Slafer *et al.*, 2023). There is a 2089-bp deletion in the promoter region of the *PPD-D1a* allele, which is characteristic of the photoperiod-insensitive allelic variant of *PPD-D1*. As a result of the deletion, the daily cycle of gene expression is significantly modified, the phenotypic consequence of which is early heading under both short- and long-day illumination (Beales *et al.*, 2007). In contrast, for *PPD-H1*, the strongest functional polymorphism is based on an SNP in exon 6 (SNP48) or in the CCT domain (SNP22), which does not induce a shift in the diurnal cycling between insensitive and sensitive alleles, and it results in contrasting phenotypic effects of the two alleles depending on the photoperiod (Turner *et al.*, 2005; Jones *et al.*, 2008; Slafer *et al.*, 2023). It is generally accepted that, in wheat, the strongest genetic influence is exerted by the semi-dominant *Ppd-D1a* allele, followed by the dominant *Ppd-B1a* and *Ppd-A1a* alleles (Blake *et al.*, 2009; Díaz *et al.*, 2012). The activity of the *PPD-D1* gene variant determining the photoperiod-sensitive allele type follows a daily cycle under both long and short days (Beales *et al.*, 2007; Zhao *et al.*, 2016a). In the early morning hours, gene expression level is very low, then reaches its maximum in the morning hours and finally this level starts to decrease. On the other hand, photoperiod-insensitive allele types do not demonstrate this daily fluctuation, and gene activity constantly shows an elevated level, which is closely related to the increase in the activity of *TaFT1* (*VRN3*) and may also affect the decrease in the peak activity of *TaCO1* (Yan *et al.*, 2006; Beales *et al.*, 2007; Díaz *et al.*, 2012; Shaw *et al.*, 2012, 2020; Campoli and von Korff, 2014; Hyles *et al.*, 2020; Gauley *et al.*, 2024). However, there is little information available on the extent to which different allele types of the *PPD-I* gene regulate floral initiation (Beales *et al.*, 2007; Shaw *et al.*, 2012, 2013; Boden *et al.*, 2015; Gauley and Boden, 2021). It is well known that photoperiod-insensitive allele types significantly reduce spikelet number, floret number and fertility, which are key factors in determining yield potential (Boden *et al.*, 2015; Prieto *et al.*, 2018a; Perez-Gianmarco *et al.*, 2019). Gauley *et al.* (2024) identified a bZIP and an ALOG transcription factor that suppress flowering and modulate spikelet number and architecture. This new knowledge may help breeders to increase yield potential (Prieto *et al.*, 2018a; Perez-Gianmarco *et al.*, 2019).

There is also little information available on how environmental factors – other than photoperiod – influence the daily activity rhythms of the two allele variants and how they impact flowering.

Circadian clock

The regulatory mechanism of the plant circadian rhythm has already been significantly explored in *Arabidopsis*, and many homologous genes have been described in wheat (Peng *et al.*, 2015), but only a few of them have been studied in detail (Kiseleva and Salina, 2018). Even less information is available

on the internal relationship between the genes responsible for the circadian rhythm, developmental genes and light-sensing receptors in cultivated wheat varieties, and how these gene interactions are influenced by environmental elements, such as ambient temperature and light spectral composition, which fundamentally affect the process of intensive stem elongation. A better understanding of these processes may enhance the ability to manipulate the adaptive capacity of cereals and thereby their productivity and geographical distribution. The circadian rhythm is an internal control mechanism (autonomous oscillator) by which plants coordinate their internal biological processes with the daily changes in temperature and light conditions of the external environment (Johansson and Staiger, 2014; Ford *et al.*, 2016). It also participates in the regulation of photosynthesis, carbohydrate synthesis, and biotic and abiotic stress responses (Bläsing *et al.*, 2005; Fowler *et al.*, 2005; Takeuchi *et al.*, 2014; Hyles *et al.*, 2020; McClung, 2021). In *Arabidopsis*, the core circadian clock consists of three interconnected major transcriptional/translational feedback loops (negative and positive) that shape the daily rhythm of gene expressions (McClung, 2006, 2021; Hsu and Harmer, 2014). Therefore, morning, daytime and evening/night transcriptional loops can be distinguished (Bendix *et al.*, 2015). *CIRCADIAN CLOCK-ASSOCIATED 1* (*CCA1*) and *LATE-ELONGATED HYPOCOTYL* (*LHY*) genes encoding an Myb transcription factor have their maximum expression in the early morning hours (Schaffer *et al.*, 1998; Cao *et al.*, 2021). Then, expression of the *PSEUDORESPONSE REGULATOR* [*PRR* – *PRR3*, *PRR5* (*PRR59* and *PRR95* in monocotyledons), *PRR7* (*PRR37* and *PRR73* in monocotyledons), *PRR9* and *TIMING OF CAB EXPRESSION1* (*TOC1/PRR1*)] genes also increases until the evening hours (Farre *et al.*, 2005; Takata *et al.*, 2010; Cao *et al.*, 2021). In the morning, the *CCA1* and *LHY* genes inhibit the expression of the *TOC1* and EC [evening complex – *ARRHYTHMO* (*LUX*), *EARLY FLOWERING 3* (*ELF3*), *EARLY FLOWERING 4* (*ELF4*)] genes. In the late afternoon, the expression of *TOC1* increases, which reduces the expression of *CCA1* and *LHY* (negative feedback loop) and also affects its own function, reducing its activity (Schaffer *et al.*, 1998; Wang and Tobin, 1998; Matsushika *et al.*, 2000; Strayer *et al.*, 2000; Alabadi *et al.*, 2001; Hazen *et al.*, 2005; Huang *et al.*, 2012a; Bendix *et al.*, 2015). *LUX*, and *ELF3* and *ELF4* show maximum expression in the evening and night respectively (Dixon *et al.*, 2011; Herrero *et al.*, 2012; Hyles *et al.*, 2020; Cao *et al.*, 2021) and inhibit the function of *PRR5*, *PRR7*, *PRR9*, *TOC1*, *GIGANTEA* (*GI*) and *NIGHT LIGHT-INDUCIBLE AND CLOCK-REGULATED1* (*LNK1*) genes (Kolmos *et al.*, 2009; Dixon *et al.*, 2011; Helfer *et al.*, 2011; Chow *et al.*, 2012; Herrero *et al.*, 2012); as a result, inhibition of the *CCA1* and *LHY* genes is reduced and a new daily cycle begins (Johansson and Staiger, 2014). The circadian rhythm also plays a key role in the regulation of daylength sensitivity among both monocotyledonous and dicotyledonous plants, as it affects the expression of *CO*, *FT* and *GI* genes (central regulatory elements) (Fowler *et al.*, 1999; Kardailsky *et al.*, 1999; Kobayashi *et al.*, 1999; Samach *et al.*, 2000; Distelfeld *et al.*, 2009a; Lazaro *et al.*, 2015; Li *et al.*, 2024). Two homologues of the *CO* gene have already been described in wheat (*TaCO1* and *TaCO2*), but their effect on flowering time is still poorly understood (Chen *et al.*, 2014). The opposite regulation (positive/negative) of *CO* on the expression of *FT* (depending

on the photoperiod-insensitive and photoperiod-sensitive alleles of the *PPD1* was observed in both barley and wheat independently of daylength (Campoli et al., 2012a; Alqudah et al., 2014; Johansson and Staiger, 2014; Mulki and von Korff, 2016; Shaw et al., 2020). Daily variation in the expression pattern and level of the *TaCO1* was also described (Shaw et al., 2013). A decrease in the expression of this gene was observed after the start of illumination; then from 3 to 6 h after this period, the transcription level showed a continuous rise until 15–18 h. The *TaHDI* gene has been described in wheat as an orthologue of *CO* (Hyles et al., 2020). Similar to *CO* in *Arabidopsis*, a daily expression pattern (with a peak value during the day) can be observed in *TaHDI* under long-day illumination. The daily rhythm of the wheat *GI* is significantly influenced by daylength (Zhao et al., 2005). It is assumed that the *GI* of wheat may have a positive effect on *CO* and indirectly also on the *FT* gene, which can result in early heading (Zhao et al., 2005; Li et al., 2024). Li et al. (2024) established a complex relationship (a combination of inhibitory and inductive processes) between *GI* and *VRN2*, as the daytime expression of *VRN2* in tetraploid wheat *gi-2* mutant lines differed compared to the wild-type. Furthermore, in the mutant lines, the time required for heading increased significantly compared to the wild-type, a phenomenon that became even more pronounced in the case of the dominant allele type of *VRN2*. Although *TaGI* is homologous to *GI* in *Arabidopsis* and has a similar function in wheat (regulation of photoperiod sensitivity), the regulatory mechanism is different in the two species (Li et al., 2024). It was found that expression maximum of wheat *TaPRR59* and *TaPRR95* is in the morning hours, which corresponds to the expression peak value of the homologous gene in rice (Kiseleva et al., 2022; Rees et al., 2022). Furthermore, the expression pattern of *TaPRR59* and *TaPRR95* resembled the transcription pattern of *PRR5* and *PRR9* in *Arabidopsis* (Kiseleva et al., 2022; Rees et al., 2022). The expression pattern of *TaPRR73* seems to show similarities to *PRR7* in *Arabidopsis*, which may indicate conservation of the functions of homologous genes between species (inhibition of *LHY/CCA1*) (Kiseleva et al., 2022). During characterization of *TaTOC1* (*TaPRR1*) identified in wheat, it was found that it has a maximum peak expression value in the evening (Zhao et al., 2016b; Rees et al., 2022), which parallels the daily pattern of activity of the homologous gene in *Arabidopsis* (James et al., 2008; Rees et al., 2022). Although several haplotypes of this gene have been described, which have been proven to be related to agronomic traits (Zhao et al., 2016b), the signalling mechanism and interaction system of this gene are not yet known (Kiseleva et al., 2022). In wheat, a homologous *LUX* (*WPCL1*) gene has been described as a repressor of *PPD1* and *VRN2* (Mizuno et al., 2016). Furthermore, Nishiura et al. (2018) demonstrated that the upregulation of *VRN1* expression after vernalization occurred in the absence of *LUX* expression. *VRN1* was upregulated in the *LUX* gene deletion mutant (*exe3*), which resulted in extremely early flowering after vernalization, both in long and short days. Thus, the direct regulation of *VRN1* by the circadian pathways independent of the vernalization pathways has also been identified (Nishiura et al., 2018). The wheat *ELF3* gene also exerts an inhibitory effect on *PPD1* during the night period (Alvarez et al., 2016, 2023), a phenomenon that was also confirmed in *Brachypodium distachyon* (Woods et al., 2023). The mutations described in this gene led to the

constitutive upregulation of *PPD1*, which was associated with early heading regardless of daylength. Furthermore, *TaELF3* has a negative effect on *TaG11* that is consistent with the function of its homologous gene in *Arabidopsis* (Yu et al., 2008; Zikhali et al., 2016). Wittern et al. (2023) showed that *ELF3* is expressed in wheat in the morning period and not in the evening as in *Arabidopsis*, and consequently the role of *ELF3* in circadian rhythm regulation is likely to differ between the two species. Furthermore, the co-expression of *ELF3* and *LUX* is not observed at dusk, which also suggests that the mechanism of the circadian oscillator in wheat might differ from that in *Arabidopsis*. Therefore, *ELF3* is an important regulator of various physiological and developmental processes and its different allele types may help to improve plant adaptation, which will be essential for plant breeding (Zahn et al., 2023). In barley, one such promising allele might be the exotic *ELF3* allele type observed by Maurer et al. (2016), Herzig et al. (2018) and Zahn et al. (2023), differing by only one nucleotide from the cultivated *ELF3* allele at the *ELF3* locus and accelerates the rate of plant development compared to the cultivated *ELF3* allele.

Light perception

The spectral composition of the light perceived by plants depends on altitude, latitude, seasons, and climatic and atmospheric factors. During the day (from dawn to dusk), the spectral energy distribution of sunlight changes, so the quality of light also contributes to the precise determination of daylength regulation and circadian rhythm (Morgan and Smith, 1981; Hyles et al., 2020). In *Arabidopsis*, several different types of photoreceptors may be distinguished, such as red and far-red light-sensing phytochromes (*PHY* – *PHYA*, *PHYB*, *PHYC*, *PHYD* and *PHYE*), cryptochromes (*CRY1* and *CRY2*), phototropins (*PHOT1* and *PHOT2*), the LOV domain-containing F-box proteins (*ZEITLUPE/ZTL*, *FLAVIN-BINDING KELCH REPEAT F-BOX 1/FKF1*, and *LOV KELCH PROTEIN 1* and *2/LKP1* and *LKP2*), blue light sensors and *UVB-RESISTANCE 8* (*UVR8*), which is a special UV-B receptor (Guo et al., 1998; Yu et al., 2010; Liu et al., 2011; Ito et al., 2012; Chen et al., 2014; Pham et al., 2018; Sanchez et al., 2020; Cao et al., 2021). The most important photoreceptors in wheat are phytochromes (*PHYA*, *PHYB* and *PHYC*) and cryptochromes (*CRY1* and *CRY2*). In *Arabidopsis*, *PHYA*, *PHOT1*, *PHOT2*, *CRY1*, *CRY2*, *FKF1* and *UVR8* have a positive effect on flowering (Valverde et al., 2004; Sawa et al., 2007; Liu et al., 2011; Arongaus et al., 2018; Kong and Zheng, 2020), while *PHYB*, *PHYC*, *PHYD*, *PHYE*, *ZTL* and *LKP2* negatively influence this process (Devlin et al., 1998, 1999; Schultz et al., 2001; Monte et al., 2003; Valverde et al., 2004; Takano et al., 2005; Kim et al., 2007; Chen et al., 2014). In wheat, by contrast, *PHYC* and *PHYB* play a positive regulatory role in the control of flowering under long-day illumination, while the role of *PHYA* is unknown (Chen et al., 2014; Pearce et al., 2016; Kiseleva and Salina, 2018). There is also no information on possible wheat homologous genes *PHOT*, *UVR8* and *FKF1* (Cao et al., 2021). Kiseleva et al. (2022) highlighted the difference in the expression pattern of the *ZTL* and *LKP2* homologous genes of wheat and *Arabidopsis*. In barley, the positive correlation of *HvPhyC* with *HvFT1* promoting the reproductive transition of the floral meristem has already

been described, an effect that was independent of the circadian cycle and *HvCO1* (Nishida *et al.*, 2013a). According to other studies, however (Pankin *et al.*, 2014), *HvPhyC* had an effect on the circadian oscillation, and it was also related to *PPD-H1*, thus promoting flowering. Similarly, in diploid wheat (*Triticum monococcum*), *PHYB* and *PHYC* upregulate *PPD1* during long days, which results in early flowering through the activation of *FT1* (*VRN3*) and *CO* (Chen *et al.*, 2014; Pearce *et al.*, 2016). In *Arabidopsis*, the photoreceptor *PHYB* has been described also to function as a temperature signal transmitter (Jung *et al.*, 2016; Legris *et al.*, 2016). However, this has not yet been investigated in temperate cereals (Cao *et al.*, 2021). The regulatory mechanisms of *TaCRY1* and *TaCRY2* have also not been investigated. In *Arabidopsis*, these two genes also play an important role in proper functioning of the internal oscillator (Yu *et al.*, 2010; Sanchez *et al.*, 2020). It has been described that *CRY2* positively affects one of the genes responsible for regulating the circadian rhythm (*CO*), which, however, also depends on the photoperiod (Guo *et al.*, 1998; Suárez-López *et al.*, 2001).

Ambient temperature perception (thermosensory)

This section summarizes the genetic regulatory mechanism of the optimal environmental temperature (between 17 and 23 °C). Temperatures outside of this range can trigger either developmental responses as was discussed in the section on the vernalization pathway or various stress responses in plants (Porter and Gawith, 1999; Acevedo *et al.*, 2009). The latter is not the aim of this review. Slafer and Rawson (1995) described that in wheat, raising the temperature from 10 to 19 °C accelerated reproductive development, whereas temperatures above 19 °C delayed terminal spikelet initiation and reduced the number of spikelet primordia. The average optimum temperature required for grain filling was found to be around 20 °C, but a temperature above 35 °C is harmful (Porter and Gawith, 1999). So lower or higher than optimal temperatures inhibit growth and reproductive development, but this effect is strongly modified by daylength (Hemming *et al.*, 2012). A higher ambient temperature (25 °C) was observed to have inhibited reproductive development with non-inductive daylength (especially in the early development phases), but accelerated the reproductive phase with inductive daylength (Rawson and Richards, 1993; Kiss *et al.*, 2017). This may be a form of adaptive advantage for temperate plants (Jacott and Boden, 2020). Although an increasing number of detailed results are available on the perception of the cold effect (vernalization) by plants and the molecular genetic mechanism of regulation, the related effects of the ambient temperature (as a secondary environmental factor) have been much less well explored. In *Arabidopsis*, several genes have already been identified to be linked to ambient temperature sensing. These include red and far-red light-sensing phytochromes (*PHY*), blue light-sensing cryptochromes (*CRY*), *UVR8*, genes involved in GA biosynthesis, and *SHORT VEGETATIVE PHASE* (*SVP*), *PRR7*, *PRR9*, *GI*, *CO*, *LUX* and *ELF3* genes (Samach *et al.*, 2000; Halliday *et al.*, 2003; Valverde *et al.*, 2004; Salome and McClung, 2005; Samach and Wigge, 2005; Fernández *et al.*, 2016; Findlay and Jenkins, 2016). At low temperatures, the transcriptional repressor *ELF3* forms a complex with the *LUX*

and *ELF4* genes preventing the activation of *FT* that is necessary for flowering. In response to an increase in temperature, the *ELF3* protein undergoes a molecular structural change that results in the dissociation of the repressor complex and, consequently, in the derepression of *FT*. The PrD (Prion-like domain) structure provides a molecular switch that allows *ELF3* to alter cell organization in response to temperature changes. In barley, it has already been observed that depending on the allele types of *PPD-H1* and *HvELF3*, 28 °C (compared to 20 °C) delayed or accelerated reproductive development (Ejaz and von Korff, 2017; Zhu *et al.*, 2023). In spring barley genotypes that carry the mutant *ppd-H1* allele, expression of *FT1* was inhibited at higher ambient temperatures, and late heading and a reduced number of grains per spike were observed compared to the control. In introgression lines carrying the wild-type *PPD-H1* or the mutant *Hvelf3* allele, on the other hand, floret primordia initiation was accelerated (through the increased activity of the *FT1*), and a higher seed number were also observed. Similarly, in spring wheat, higher ambient temperatures either reduce or do not significantly affect *FT1* expression (Kiss *et al.*, 2017; Dixon *et al.*, 2018). Furthermore, it was observed that ending of the repressive effect of *ELF3* at a higher ambient temperature (25 °C) involved an increase in the expression of the *GI*, *LUX* and *PRR* genes (Ford *et al.*, 2016). Thus, at higher temperatures, *ELF3* can play a central role in the regulation processes of photoperiod-dependent flowering (Ford *et al.*, 2016). In wheat, Ochagavía *et al.* (2019) described those differences between alleles of *TaELF3* that resulted in different levels of sensitivity to temperature, according to which precociousness in hexaploid wheat was associated with increased sensitivity to temperature in the late reproductive phase. The same study also showed a temperature-dependent inhibition of *TaGI* controlled by *TaELF3*. Genes involved in vernalization also show a strong interaction with temperature (Kiss *et al.*, 2017; Dixon *et al.*, 2019). Delayed flowering of winter wheat genotypes (following exposure to higher ambient temperatures during and after cold treatment) was described to be genetically closely linked to *VRN1* (highlighting *VRN-A1*) (Dixon *et al.*, 2019). Furthermore, higher ambient temperature (25 °C) led to increased expression of *VRN2* associated with reduced levels of *VRN1* and *FT1* transcripts compared to gene activities at moderate (18 °C) and low (11 °C) temperatures (Kiss *et al.*, 2017; Dixon *et al.*, 2019). The gene expression values influenced by the ambient temperature observed by the authors were significantly dependent on the photoperiod-insensitive and photoperiod-sensitive allele type of *PPD-D1*. Allele types of *VRN1* also influence the expression of flowering-promoting factors in barley. In the treatments at higher ambient temperature, the inhibition of expression of *FT1* was more pronounced in the winter compared to the spring genotypes, related to a stronger repression of *VRN1* (Ejaz and von Korff, 2017).

Earliness *per se*

Allelic variants of ‘Earliness *per se*’ (*Eps*) genes can cause differences in flowering time of a few days, independent of environmental effects (Worland, 1996; Snape *et al.*, 2001; Bullrich *et al.*, 2002; Zikhali *et al.*, 2014). A close relationship was also established with the *PPD* and circadian genes,

so their interrelated effect determines the final level of photoperiod sensitivity of a given genotype (Worland, 1996; Hyles et al., 2020). The most important function of the *Eps* genes is fine-tuning of flowering time (Hoogendoorn, 1985; Valárik et al., 2006; Griffiths et al., 2009; Horváth et al., 2023). Thus, some allelic variants of these genes may be used in the creation of new genotypes that, with their earliness, can avoid the early summer dry period, thus increasing the productivity of the varieties, and therefore also increasing crop security. ‘Earliness per se’ is a quantitative trait determined by a number of genes with smaller effects (Kato and Wada, 1999). In bread wheat, numerous quantitative trait locus (QTL) analyses have already indicated the existence of genes on most chromosomes that may be associated with earliness (Snape et al., 2001; Hanocq et al., 2007; Chen et al., 2010; Basavaraddi et al., 2021). These QTL effects were independent of the effects of the main genes of the *VRN* and *PPD* regulatory pathways. However, Horváth et al. (2023) identified several *eps* loci in a wheat association panel during field developmental studies, the detectability of which was closely related to the allele type of *PPD-D1*. In most of the cases, the genes behind these earliness loci are not yet known. However, several examples are available where the gene was cloned and characterized and, in some cases, proved to belong to the circadian clock. Zikhali et al. (2016) identified that the gene of the *Eps-3A^m* locus in *Triticum monococcum* is orthologous to *LUX/PCL1* of *Arabidopsis* (Shindo et al., 2002; Gawroński and Schnurbusch, 2012; Mizuno et al., 2012; Gawroński et al., 2014). The photoperiod-insensitive mutant version of this gene was associated with early heading and showed increased expression of the *TmFT*, *Ppd-1*, *WCO1* and *TmHd1* genes, and it was also associated with sensitivity to temperature, similar to the *Eps-A^{m1}* (*T. monococcum* 1A^m) gene (Bullrich et al., 2002; Lewis et al., 2008; Gawroński et al., 2014). Bullrich et al. (2002) identified a QTL in a mapping population that was closely linked to a major *Eps* gene (*Eps-A^{m1}*). This is one of the best characterized *Eps* loci that is located on chromosome 1A^m of *T. monococcum* (Bullrich et al., 2002; Valárik et al., 2006; Lewis et al., 2008; Faricelli et al., 2016) and is considered to be an orthologue of *TaELF3* (Alvarez et al., 2016; Wang et al., 2016). The early allele type of this gene (*Eps-A^{m1-e}*) significantly accelerated the time required for flowering, while the late allele type (*Eps-A^{m1-l}*) significantly delayed it. The different temperature optimum of these two allele types was also described by Bullrich et al. (2002) and verified by Appendino and Slafer (2003) in *aestivum* wheats. In hexaploid wheat, Zikhali et al. (2014) detected a QTL responsible for earliness on chromosome 1DL (*Eps-D1*, homologous to *Eps-A^{m1}*) of hexaploid wheat, the effect of which was confirmed in NIL populations under both field and controlled conditions. They also identified *TaELF3* as the gene responsible for this effect (Zikhali et al., 2016). In those lines that carried the deletion of the *Eps-D1* gene, the expression of *TaELF3* was significantly reduced and the expression of *TaGI* changed compared to the wild-type. The temperature-dependent relationship between the early and late allele type of *Eps-D1* and several yield-related components with an emphasis on the number of fertile florets, leaf development dynamics and heading time was analysed in detail (Prieto et al., 2020). *Eps* genes probably affect almost all development phases, such as the vegetative/generative transition, early and late spike differentiation, the stem elongation

phase, heading, and spike fertility, which also have a significant role in determining grain yield (Lewis et al., 2008; Griffiths et al., 2009; Ochagavía et al., 2018; Prieto et al., 2018b). Buckley et al. (2024) found that the deletion of *Eps-D1* affects ageing processes and the protein content of the grains.

Gibberellin response pathways

Plant height is also a key factor determining environmental adaptation. The regulation mechanism of endogenous GA hormone synthesis plays a prominent role in the formation of the final plant height. Gibberellins are pentacyclic diterpene compounds that stimulate growth, so they play an important role in germination, the stem elongation phase, leaf development, the reproductive developmental phase and the regulation of various environmental stress responses (Olszewski et al., 2002; MacMillan et al., 2005; Yamaguchi, 2008; Llanes et al., 2016). Their effect is manifested in the fact that they degrade the growth-inhibiting DELLA proteins. These proteins are encoded by *GAI*, *RGA*, *RGL1*, *RGL2* and *RGL3* in *Arabidopsis*, by *SLR1* in rice, and by *RHT* in wheat (Peng et al., 1997; Ikeda et al., 2001). GA is sensed by the protein receptor *GID1* (*GIBBERELLIN-INSENSITIVE DWARF1*), which was first identified in gibberellin-insensitive dwarf mutants of rice (Ueguchi-Tanaka et al., 2005). Three *GID1* orthologues have been described in *Arabidopsis* (*AtGID1a*, *AtGID1b* and *AtGID1c*) with overlapping functions (Nakajima et al., 2006). In *AtGID1*, the triple mutant in *Arabidopsis* GA sensing did not work, and as a result, the plants became extremely dwarfed. This phenotypic effect did not appear in the single mutants, but it did in the double mutants (Griffiths et al., 2006; Iuchi et al., 2007; Willige et al., 2007). Over the last 10 years, the GA signalling mechanism by the *GID1* protein and the details of GA biosynthesis itself have been elucidated through biochemical, genetic and structural analyses in rice and *Arabidopsis* (Ueguchi-Tanaka et al., 2005; Griffiths et al., 2006; Jiang and Fu, 2007; Murase et al., 2008; Hirano et al., 2010). Seven different types of enzymes may be highlighted in GA biosynthesis, such as ent-copalyl diphosphate synthase (CPS), ent-kaurene synthase (KS), ent-kaurene oxidase (KO), ent-kaurenoic acid oxidase (KAO), GA20 oxidase, GA3 oxidase and GA2 oxidase (Yamaguchi, 2006). Orthologues of the genes responsible for the synthesis of these enzymes have already been described in wheat (Spielmeyer et al., 2004; Appleford et al., 2006; Y. Zhang et al., 2007; Khlestkina et al., 2010; Huang et al., 2012b; Tang et al., 2019) and their expressions were shown to be tissue- and developmental stage-specific (Huang et al., 2012b). The role of GA in flowering appears to be species-dependent as it promotes flower initiation in *Arabidopsis*, but inhibits this process in several perennials (Mutasa-Göttgens and Hedden, 2009). Pearce et al. (2013) demonstrated that in wheat, *VRN3* also upregulates GA biosynthesis through *GA20ox* and inhibits the expression of *GA20ox1* through indirect and direct ways. The increased level of GA and the transcriptional activity of *VRN1* upregulate the function of the *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1-1* (*SOC1-1*) and *LEAFY* (*LFY*) genes, a process required for normal spike development (Pearce et al., 2013). In hexaploid wheat, GA signalling factors and DELLA proteins are also encoded by *RHT* (Peng et al., 1999). The DELLA

genes are located at three homologous loci, *Rht-A1*, *Rht-B1* (formerly *RHT1*) and *Rht-D1* (formerly *RHT2*) on chromosomes 4A, 4B and 4D (Börner *et al.*, 1996; Flintham *et al.*, 1997; Peng *et al.*, 1999; Febrer *et al.*, 2009). In the *Rht-B1b* and *Rht-D1b* GA-insensitive (mutant) alleles, degraded proteins are produced that are unable to form the appropriate GA–GID–DELLA protein complex, and as a result, the DELLA protein cannot be degraded, but instead accumulates and inhibits the growing processes (Peng *et al.*, 1999; Hyles *et al.*, 2020). These mutant alleles reduce the length of the internodes that results in reduced plant height (Keyes *et al.*, 1989; Hoogendoorn *et al.*, 1990) and can also be associated with reduced leaf size (Allan, 1989; Ellis *et al.*, 2004). Although the decrease can be observed between all internodes, the largest absolute decrease is found in the last internode length (Hoogendoorn *et al.*, 1990). The shorter last internode allows more assimilates to be used for growth and development of the differentiating spikelet (Youssefian *et al.*, 1992), and as a result, more fertile florets can be formed that also increase the potential seed number. Recently, Song *et al.* (2023a) identified an *Rht-B1* null mutant in wheat segregation lines where a natural deletion of about 500 kb within the *ZnF-B* gene (encoding a RING-type E3 ligase) was observed. This deletion resulted in semi-dwarf plants with more compact plant architecture and significantly increased grain yield (up to 15.2 %) in field experiments compared to *Rht-B1b* and *Rht-D1b* mutants. Further genetic analyses confirmed that deletion of *ZnF-B* in the absence of *Rht-B1b* and *Rht-D1b* alleles caused the semi-dwarf trait by weakening brassinosteroid (BR) sensing. Hence, *Rht-B1* null mutants can be a promising source for the production of new cultivars with high yield and desired height. Dong *et al.* (2023) reported that *GLYCOGEN SYNTHASE KINASE 3* (*GSK3*) phosphorylates *Rht-B1b* modification through the BR pathway, thus causing reduced plant height. Other authors (Li *et al.*, 2010; Chen *et al.*, 2020b) described that the BR sensing pathway in *Arabidopsis* is also related to the regulation of flowering time; however, the molecular–genetic regulatory mechanism of this process remains unclear. In addition, Cui *et al.* (2023) demonstrated that *GSK3* is in physical contact with *VRN1* and regulates its intracellular accumulation through *VRN3*. Other *RHT*s have also been identified as individual allelic variants of *RHT1* and *RHT2* (*RHT3*, *RHT4*, *RHT5*, *RHT6*, *RHT7*, *RHT8*, *RHT9*, *RHT10*, *RHT11*, *RHT12*, *RHT13*, *RHT14*, *RHT15*, *RHT16*, *RHT17*, *RHT18*, *RHT19*, *RHT20*, *RHT21*, *RHT22*, *RHT23*, *RHT24*, *RHT25*, *RHT26* and *RHT27*); although their exact genetic regulation is not yet sufficiently known, their effect on plant height has already been proven (Flintham and Gale, 1983; Konzak, 1987; Loskutova, 1998; Peng *et al.*, 1999, 2011; Ellis *et al.*, 2004, 2005; Haque *et al.*, 2011; Divashuk *et al.*, 2012; Li *et al.*, 2012; Bazhenov *et al.*, 2015; Chen *et al.*, 2015; Lu *et al.*, 2015; Würschum *et al.*, 2017; Yan and Zhang, 2017; Du *et al.*, 2018; Ford *et al.*, 2018; Mo *et al.*, 2018; Mohan *et al.*, 2021; Zhao *et al.*, 2021; Song *et al.*, 2023b; Liu *et al.*, 2024). There is also little information available about the mechanism of regulation and the relationship between *RHT* genes and other genetic components responsible for flowering regulation in cereals.

Use of *Rht-B1b* and *Rht-D1b* alleles in new breeding lines ('Green Revolution' – 1960/1970s) made it possible to replace the tall, lodging-sensitive varieties in the past with short, less lodging-sensitive varieties. The introduction of these genes

resulted in higher average grain yields, due to which those cultivars harbouring any combinations of *Rht* mutant alleles spread rapidly in breeding and cereal production (Gao and Chu, 2020). Combining the adequate alleles of the *RHT* genes is extremely important in breeding to avoid adverse phenotypic effects. It has been described that combining the *Rht-B1b* and *Rht-D1b* alleles with the *RHT8* gene resulted in extremely dwarfed plants with reduced spike fertility rates (Worland and Law, 1986). The allelic combinations of *RHT15* and *RHT1* reduced the grain yield per plant (Zhao *et al.*, 2023). Cseh *et al.* (2024) also observed that *Rht-B1* and *Rht-D1* mutants are prone to meiotic aberrations (reduced spike fertility rate) even at optimal temperatures and showed a higher level of sensitivity to heat stress than the taller genotypes. In addition, the reduced fertility may be linked to the reduced recombination level of homologous chromosomes and the frequency of defective chromosome separations. Regarding cereal development, genetic regulation of GA biosynthesis lies in the intricate regulation cascade system of plant development, including the vegetative–generative transitions and the stem elongation phase, which is much less well understood.

Ageing pathway

In *Arabidopsis*, senescence-related genetic factors are also among the most important elements of flowering regulation (Rehman *et al.*, 2023) and several *SQUAMOSA PROMOTER BINDING LIKE* (*SPL*) genes regulated by miRNAs have now been described (Xu *et al.*, 2016). In *Arabidopsis*, the concentration of *SPL* transcription factors increases continuously with ageing (Fornara *et al.*, 2010). These factors promote flowering and ripening, and during this process they also induce the expression of several transcription factors [*LFY*, *FRUITFULL* (*FUL*) and *SOC1*]. miRNAs include short (21–24 nucleotides) non-coding nucleic acid sequences that participate in gene expression regulation (through mRNA cleavage or translation inhibition) (Bartel, 2009; Chellappan *et al.*, 2010). miR156 and miR172 are one of the miRNA families showing the greatest degree of conservation in plants (Rehman *et al.*, 2023). *SPL* proteins correlate negatively with miR156, the level of which is significantly higher in young than in older leaves (Fornara *et al.*, 2010), while *SPL* genes activate the expression of miR172 in leaves. An increased level of miR172 inhibits the expression of *APETALA2-like* (*AP2L*) genes (flowering-inhibitory transcription factors) promoting flowering competence (Wu *et al.*, 2009; Debernardi *et al.*, 2022; Li *et al.*, 2024). Furthermore, it was described that the synthesis of miRNAs is a temperature-dependent process (e.g. miR156 and miR169 are upregulated at 16 °C) thus preventing precocious flowering at sub-optimal temperatures (Kim *et al.*, 2012; Quiroz *et al.*, 2021). Other miRNA families have already been identified in wheat by genome-wide association analysis (Yao *et al.*, 2007; Sun *et al.*, 2014). However, the functions of the identified miRNAs and their role in genetic regulation of plant development are not yet sufficiently detailed. The wheat miR5200 is homologous to that described in *Brachypodium distachyon* and it also inhibits the expression of *FTI* in short-day conditions (Wu *et al.*, 2013; Li *et al.*, 2014; Pearce *et al.*, 2016). These studies also demonstrated that *PHYC* of wheat has a negative effect on this

molecule. An miRNA has also been described in wheat (tae-miR408) associated with flowering time (Zhao *et al.*, 2016b). This molecule exerts a negative effect on the *TaTOC1* circadian rhythm gene, and as a result, the expression level of *TaFT1* that plays an important role in flowering regulation also increases.

Why is it so important to study the stages of plant development in wheat?

Vernalization requirement and photoperiod sensitivity are the basic components influencing plant developmental phases in cereals grown under continental conditions. After the saturation of these major developmental factors, there are other components (circadian rhythm, light perception, hormonal regulation and *earliness per se*) that sense subsidiary environmental signals, such as light intensity and ambient temperature. This continuous adjustment to environmental conditions ensures the fine-tuning of adaptive plant growth (Fornara *et al.*, 2010). As climatic anomalies (taken here to mean weather conditions that are unusual at any given time of year) increase both in magnitude and in frequency, they affect not only fine-tuning mechanisms but also the major plant developmental responses (Porter and Semenov, 2005). It is therefore essential to establish the extent to which disturbances in plant developmental patterns negatively affect yield formation and to obtain detailed physiological and genetic knowledge on the starting date and length of various plant developmental phases. This will enable breeders to modify both the transition from the vegetative to the generative phase of the genotypes by changing the scale of photoperiod-sensitivity and vernalization requirements and the effectiveness of fine-tuning mechanisms (González *et al.*, 2005; Borràs *et al.*, 2009; Chen *et al.*, 2009, 2010; Maurer *et al.*, 2016; Zahn *et al.*, 2023). The length of the various developmental phases is an important factor determining the extent to which the yield potential of a genotype may be achieved under a given set of ecological conditions (Slafer and Rawson, 1996; Araus *et al.*, 2002; González *et al.*, 2005; McMaster, 2005; Borràs *et al.*, 2009; Chen *et al.*, 2009; Foulkes *et al.*, 2011). One such adaptation process is a time shift in the rapid stem elongation phase (Fischer, 1985; Slafer and Rawson, 1994; Reynolds *et al.*, 2009; García *et al.*, 2011). The later timing of stem elongation helps to avoid frost damage in early spring, whereas earlier maturity helps to avoid hot dry weather during summer. Similarly, the relative duration of any two consecutive phases can be also important in determining the various yield components. A longer vegetative phase generates more biomass (due to the longer nutrient storage period), and an extended stem elongation phase is required to achieve a higher number of fertile florets or spikelets, whereas a longer grain-filling period may lead to increased grain weight in the spikes (Kirby, 1988; Slafer and Rawson, 1996; Miralles and Richards, 2000; Whitechurch and Slafer, 2001, 2002; Araus *et al.*, 2002; González *et al.*, 2002, 2003, 2005; Kiss *et al.*, 2011; Dreccer *et al.*, 2014; González-Navarro *et al.*, 2015, 2016). The time between first node appearance and the start of rapid stem elongation has a significant effect on the number of reproductive tillers, and a close association was observed between the second half of rapid stem elongation (from the boot stage to heading) and the number of spikelets per spike (Miralles and Richards, 2000; Whitechurch and Slafer, 2001,

2002; Kiss *et al.*, 2011, 2014a). Guo *et al.* (2018) further subdivided the stem elongation phase into seven sub-phases to investigate their effects on yield components. The most important finding of their study was the potential strategies for controlling the narrow time windows (sub-phases) during the stem elongation phase to increase floret fertility and grain number. At the time of stem elongation, it is important that the development of node initiation and elongation of the internodes are appropriate for the yield. However, it is still unclear how these events are spatiotemporally coordinated (Huang *et al.*, 2024). This approach to cereal stem development may be traced back to information obtained from diploid barley. The main body axis of barley represents a simple and continuous segmentation of phytomers (apex-derived organ form) wherein both vegetative and reproductive organs coexist at opposite ends (Huang *et al.*, 2024). In addition to the phytohormones (such as gibberellin), the *FLOWERING LOCUS T* (*FT*)/*TERMINAL FLOWERING 1* (*TFL1*) family genes also play a crucial role in the formation of plant structure (Taoka *et al.*, 2011; Eshed and Lippman, 2019; McKim, 2020). In barley, the *HvFT1* gene integrates signals from vernalization (*VERNALIZATION 1, 2* – *VRN-H1*, *VRN-H2*), photoperiod (*PHOTOPERIOD 1* – *PPD-H1*) and circadian (*EARLY FLOWERING 3* – *HvELF3*) regulatory pathways for floral induction (Turner *et al.*, 2005; Faure *et al.*, 2012; Boden *et al.*, 2014; Deng *et al.*, 2015). Mutations in these flowering time genes may cause significant changes in both vegetative and reproductive phytomeric iterations (Huang *et al.*, 2023). However, little information is available on how phytomer initiation and elongation are coordinated during morphogenesis (Huang *et al.*, 2024). The effects of vernalization requirement and photoperiod sensitivity on plant developmental stages are much better known than the effects of secondary environmental elements (ambient temperature, light spectra). Temperature affects each phase, and a higher ambient temperature generally accelerates growth and development rates in crop species (Slafer and Rawson, 1994, 1995; Atkinson and Porter, 1996; Slafer *et al.*, 2015). However, it is not clear whether the response to temperature is independent of growth rate and development (Kronenberg *et al.*, 2021). In relation to the light spectrum, it should be pointed out that the far-red spectrum increases plant internodal length, petiole length, plant height and gibberellin content, among others (Kurepin *et al.*, 2010; Hitz *et al.*, 2019). The effect of this spectrum has been studied mainly as shade avoidance responses, which are changes in the growth and development pattern of plants caused by shifts in the light spectrum (in the red:far-red light ratio) caused by neighbouring vegetation (Casal *et al.*, 1986). In *Arabidopsis*, the regulation of this process is well documented; however, in wheat, it remains limited (Wille *et al.*, 2017). In *Arabidopsis*, sunlight activates *PHYB* and *CRY1* to repress shade avoidance responses. The loss-of-function mutants of these photosensory receptors show shade avoidance responses under full sunlight (Mazzella and Casal, 2001). Warm conditions reduce the activity of *PHYB*, which operates as a temperature sensor and further increases the activities of *PHYTOCHROME INTERACTING FACTORS* (*PIF4* and *PIF7*) by independent temperature sensing mechanisms (Casal and Fankhauser, 2023).

In summary, a more comprehensive and quantitative understanding of the physiological and genetic determinants of time

to heading and the partitioning of time among the phenophases of preflowering development would allow the fine-tuning of adaptation and the optimization of development for maximum yield potential under both present and future conditions. Extending the duration of phase intervals with a decisive influence on yield components without modifying the total time to anthesis has been proposed as a promising breeding tool, but this requires detailed information on the mechanism of the genetic and environmental regulation of the start and duration of various phases and their interactions (Chen *et al.*, 2009, 2010). However, variations in environmental parameters in different years under field conditions may produce considerable variability in phenotypic responses, often leading to contradictory results (Snape *et al.*, 1985; Worland, 1996; Worland *et al.*, 1998; Kato *et al.*, 2000). The importance of this research field is also underlined by the fact that neither the changes caused by global climatic change on local climate conditions nor their effects on plant developmental strategies can be exactly predicted (Kiss *et al.*, 2011).

CONCLUSIONS

Studying the genes that determine flowering in *Arabidopsis* provides a good foundation for mapping orthologous genes in wheat. This can be of great help for further dissecting and analysing QTLs and genes identified by different molecular genetic and genomic tools as well as for studying their functions and interactions in cereals. This review has provided an overview of the regulatory system of the most important genes that determine the vegetative–generative transition of wheat shoot apex (Fig. 2; Table 1). These genes may be organized around four main regulatory pathways, such as *earliness per se*, light/photoperiod sensitivity, vernalization (cold requirement), hormonal (GA synthesis) and ageing regulation. The results so far have proven the significant differences between the genes determining the vernalization processes of *Arabidopsis* and crop plants, but the regulatory processes show a high degree of similarity in both mono- and dicotyledonous plants. In wheat, the genetic factors of the vernalization, photoperiod and circadian rhythm control pathways (especially the *VRN1*, *VRN2*, *VRN3*, *PPD1*, *CO* and *GI* genes) integrate signals from the environment (vernalizing temperature, daylength), defining the vegetative–generative transition phase, while the importance of GA synthesis and earliness regulation lies in the fine-tuning of further plant development dependent on a set of partially different environmental factors (ambient temperature, daylength, light intensity, spectral composition of light). This complex process has a fundamental effect on the intensive stem elongation phase, which determines various parameters of grain yield. Several studies have already reported on the major regulatory genes responsible for environmental adaptation in wheat and the role of their allelic variants. These results have been established by experiments with diploid (*Triticum monococcum*) and tetraploid (*Triticum turgidum* subsp. *durum*) species with smaller genome sizes or with specific crossing lines (RIL, NIL, mutant and transgenic lines). However, this review also highlights that the current knowledge of the light and temperature control in the process of wheat heading (especially bread wheat) is not yet comprehensive, with only elements of

vernalization and photoperiod control being described in detail. Even less is known about complex regulatory pathways such as the circadian rhythm of wheat and its effect on development, the regulatory pathway of GA, or the genetic regulation of earliness and ageing. These areas are extremely difficult to study because vernalization and photoperiod responses, being the most determining, can hide the effects of other regulatory pathways. However, the number of studies linking new genes to the wheat heading process is increasing year by year, further confirming that this information will be an essential task for the future. Elucidating how the epistatic effects of particular allelic variants in different varieties may influence the expression of particular genes under different environmental conditions and how these may be linked will also be important. In summary, detailed omics-based discovery of wheat's ability to adapt may become increasingly valuable. Due to rapidly and unpredictably changing climatic effects, the need for breeders to find the genetic materials from which they can produce varieties that are most adaptable to local environmental conditions is increasing. In the future, cultivation of these varieties may ensure adequate quality and quantity of yield.

FUNDING

Funding of this research was provided by TKP2021-NKTA-06 (from the National Research, Development and Innovation Fund, financed under the TKP2021-NKTA funding scheme), and by NKFI-FK-134234 and NKFI-K-142934 (from the National Research, Development and Innovation Fund). T.K. and A.C. were supported by János Bolyai Research Scholarships of the Hungarian Academy of Sciences (BO/00396/21/4 and BO/00416/23/4, respectively).

AUTHOR CONTRIBUTIONS

T.K. and I.K. conceived the article. T.K., Á.D.H., A.C., Z.B. and K.B. wrote the first draft. All authors were involved in revision of the draft manuscript and have agreed to the final content.

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

LITERATURE CITED

- Abe M, Kobayashi Y, Yamamoto S, *et al.* 2005. FD, a bZIP protein mediating signals from the floral pathway integrator *FT* at the shoot apex. *Science* 309: 1052–1056.
- Acevedo E, Silva P, Silva H. 2009. *Wheat growth and physiology*. FAO corporate document repository. Rome: FAO, 1–31.
- Alabadi D, Oyama T, Yanovsky MJ, Harmon FG, Más P, Kay SA. 2001. Reciprocal regulation between *TOC1* and *LHY/CCA1* within the *Arabidopsis* circadian clock. *Science* 293: 880–883.
- Allan RE. 1989. Agronomic comparisons between *Rht1* and *Rht2* semidwarf genes in winter wheat. *Crop Science* 29: 1103–1108.
- Alqudah AM, Sharma R, Pasam RK, Graner A, Kilian B, Schnurbusch T. 2014. Genetic dissection of photoperiod response based on GWAS of pre-anthesis phase duration in spring barley. *PLoS One* 9: e113120.

- Alvarez MA, Tranquilli G, Lewis S, Kippes N, Dubcovsky J. 2016. Genetic and physical mapping of the earliness per se locus *Eps-A (m) 1* in *Triticum monococcum* identifies *EARLY FLOWERING 3 (ELF3)* as a candidate gene. *Functional and Integrative Genomics* 16: 365–382.
- Alvarez MA, Li C, Lin H, et al. 2023. *EARLY FLOWERING 3* interactions with *PHYTOCHROME B* and *PHOTOPERIOD1* are critical for the photoperiodic regulation of wheat heading time. *PLoS Genetics* 19: e1010655.
- Andrade L, Lu Y, Cordeiro A, et al. 2022. The evening complex integrates photoperiod signals to control flowering in rice. *Proceedings of the National Academy of Sciences of the United States of America* 119: e2122582119.
- Appendino ML, Slafer GA. 2003. Earliness per se and its dependence upon temperature in diploid wheat lines differing in the major gene *Eps-Aml* alleles. *The Journal of Agricultural Science* 141: 149–154.
- Appleford NE, Evans DJ, Lenton JR, et al. 2006. Function and transcript analysis of gibberellin-biosynthetic enzymes in wheat. *Planta* 223: 568–582.
- Araus JL, Slafer GA, Reynolds MP, Royo C. 2002. Plant breeding and water relations in C3 cereals: What to breed for? *Annals of Botany* 89 Spec No: 925–940.
- Arongaus AB, Chen S, Pireyre M, et al. 2018. *Arabidopsis* *RUP2* represses *UVR8*-mediated flowering in noninductive photoperiods. *Genes and Development* 32: 1332–1343.
- Atkinson D, Porter JR. 1996. Temperature, plant development and crop yields. *Trends in Plant Science* 1: 119–124.
- Barrett B, Bayram M, Kidwell K, Weber WE. 2002. Identifying AFLP and microsatellite markers for vernalization response gene *vrn-B1* in hexaploid wheat using reciprocal mapping populations. *Plant Breeding* 121: 400–406.
- Bartel DP. 2009. MicroRNAs: target recognition and regulatory functions. *Cell* 136: 215–233.
- Basavaraddi PA, Savin R, Wingen LU, et al. 2021. Interactions between two QTLs for time to anthesis on spike development and fertility in wheat. *Scientific Reports* 11: 2451.
- Bazhenov MS, Divashuk MG, Amagai Y, Watanabe N, Karlov GI. 2015. Isolation of the dwarfing *Rht-B1p (Rht17)* gene from wheat and the development of an allele-specific PCR marker. *Molecular Breeding* 35: 213.
- Beales J, Turner A, Griffiths S, Snape JW, Laurie DA. 2007. A Pseudo-Response Regulator is misexpressed in the photoperiod insensitive *Ppd-D1a* mutant of wheat (*Triticum aestivum* L.). *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* 115: 721–733.
- Bendix C, Marshall CM, Harmon FG. 2015. Circadian clock genes universally control key agricultural traits. *Molecular Plant* 8: 1135–1152.
- 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: 181.
- Berezhnaya A, Kiseleva A, Leonova I, Salina E. 2021. Allelic variation analysis at the vernalization response and photoperiod genes in Russian wheat varieties identified two novel alleles of *vrn-B3*. *Biomolecules* 11: 1897.
- Blake NK, Lanning SP, Martin JM, et al. 2009. Effect of variation for major growth habit genes on maturity and yield in five spring wheat populations. *Crop Science* 49: 1211–1220.
- Bläsing OE, Gibon Y, Günther M, et al. 2005. Sugars and circadian regulation make major contributions to the global regulation of diurnal gene expression in *Arabidopsis*. *The Plant Cell* 17: 3257–3281.
- Boden SA, Weiss D, Ross JJ, et al. 2014. *EARLY FLOWERING3* regulates flowering in spring barley by mediating gibberellin production and *FLOWERING LOCUS T* expression. *The Plant Cell* 26: 1557–1569.
- Boden SA, Cavanagh C, Cullis BR, et al. 2015. *Ppd-1* is a key regulator of inflorescence architecture and paired spikelet development in wheat. *Nature Plants* 1: 14016.
- Bonnin I, Rousset M, Madur D, et al. 2008. FT genome A and D polymorphisms are associated with the variation of earliness components in hexaploid wheat. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* 116: 383–394.
- Börner A, Plaschke J, Korzun V, Worland AJ. 1996. The relationships between the dwarfing genes of wheat and rye. *Euphytica* 89: 69–75.
- Börner A, Korzun V, Worland AJ. 1998. Comparative genetic mapping of loci affecting plant height and development in cereals. *Euphytica* 100: 245–248.
- Borràs G, Romagosa I, van Eeuwijk F, Slafer GA. 2009. Genetic variability in duration of pre-heading phases and relationships with leaf appearance and tillering dynamics in a barley population. *Field Crops Research* 113: 95–104.
- Brambilla V, Gomez-Ariza J, Cerise M, Fornara F. 2017. The importance of being on time: regulatory networks controlling photoperiodic flowering in cereals. *Frontiers in Plant Science* 8: 665.
- Buckley CR, Boyte JM, Albiston RL, et al. 2024. A circadian transcriptional sub-network and *EARLY FLOWERING 3* control timing of senescence and grain nutrition in bread wheat. *bioRxiv* 580927. doi:10.1101/2024.02.19.580927
- Bullrich L, Appendino ML, Tranquilli G, Lewis S, Dubcovsky J. 2002. Mapping of a thermo-sensitive earliness per se gene on *Triticum monococcum* chromosome 1A^W. *Theoretical and Applied Genetics* 105: 585–593.
- Campoli C, von Korff M. 2014. Genetic control of reproductive development in temperate cereals. In: Jacquot JP, Gadal P, Fornara F. eds. *Advances in botanical research. The Molecular Genetics of Floral Transition and Flower Development*. New York: Academic Press, 131–158.
- Campoli C, Drosse B, Searle I, Coupland G, von Korff M. 2012a. Functional characterisation of *HvCO1*, the barley (*Hordeum vulgare*) flowering time ortholog of *CONSTANS*. *The Plant Journal: for Cell and Molecular Biology* 69: 868–880.
- Campoli C, Shtaya M, Davis SJ, von Korff M. 2012b. Expression conservation within the circadian clock of a monocot: natural variation at barley *Ppd-H1* affects circadian expression of flowering time genes, but not clock orthologs. *BMC Plant Biology* 12: 97.
- Campoli C, Pankin A, Drosse B, Casao CM, Davis SJ, von Korff M. 2013. *HvLUX1* is a candidate gene underlying the *early maturity 10* locus in barley: phylogeny, diversity, and interactions with the circadian clock and photoperiodic pathways. *The New Phytologist* 199: 1045–1059.
- Cane K, Eagles HA, Laurie DA, et al. 2013. *Ppd-B1* and *Ppd-D1* and their effects in southern Australian wheat. *Crop and Pasture Science* 64: 100–114.
- Cao S, Luo X, Xie L, et al. 2020. The florigen interactor BdES43 represses flowering in the model temperate grass *Brachypodium distachyon*. *The Plant Journal* 102: 262–275.
- Cao S, Luo X, Xu D, et al. 2021. Genetic architecture underlying light and temperature mediated flowering in *Arabidopsis*, rice, and temperate cereals. *The New Phytologist* 230: 1731–1745.
- Casal JJ, Fankhauser C. 2023. Shade avoidance in the context of climate change. *Plant Physiology* 191: 1475–1491.
- Casal JJ, Sánchez RA, Deregibus VA. 1986. The effect of plant density on tillering: the involvement of R/FR ratio and the proportion of radiation intercepted per plant. *Environmental and Experimental Botany* 26: 365–371.
- Chellappan P, Xia J, Zhou X, et al. 2010. siRNAs from miRNA sites mediate DNA methylation of target genes. *Nucleic Acids Research* 38: 6883–6894.
- Chen A, Dubcovsky J. 2012. Wheat TILLING mutants show that the vernalization gene *VRN1* down-regulates the flowering repressor *VRN2* in leaves but is not essential for flowering. *PLoS Genetics* 8: e1003134.
- Chen M, Chory J, Fankhauser C. 2004. Light signal transduction in higher plants. *Annual Review of Genetics* 38: 87–117.
- Chen Y, Carver BF, Wang S, Zhang F, Yan L. 2009. Genetic loci associated with stem elongation and winter dormancy release in wheat. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* 118: 881–889.
- Chen Y, Carver BF, Wang S, Cao S, Yan L. 2010. Genetic regulation of developmental phases in winter wheat. *Molecular Breeding* 26: 573–582.
- Chen F, Gao M, Zhang J, Zuo A, Shang X, Cui D. 2013. Molecular characterization of vernalization response genes in bread wheat from the Yellow and Huai Valley of China. *BMC Plant Biology* 13: 199.
- Chen A, Li C, Hu W, et al. 2014. *Phytochrome C* plays a major role in the acceleration of wheat flowering under long-day photoperiod. *Proceedings of the National Academy of Sciences of the United States of America* 111: 10037–10044.
- Chen S, Gao R, Wang H, et al. 2015. Characterization of a novel reduced height gene (*Rht23*) regulating panicle morphology and plant architecture in bread wheat. *Euphytica* 203: 583–594.
- Chen Z, Cheng X, Chai L, et al. 2020a. Pleiotropic QTL influencing spikelet number and heading date in common wheat (*Triticum aestivum* L.). *Theoretical and Applied Genetics* 133: 1825–1838.
- Chen Y, Song S, Gan Y, Jiang L, Yu H, Shen L. 2020b. SHAGGY-like kinase 12 regulates flowering through mediating CONSTANS stability in *Arabidopsis*. *Science Advances* 6: eaaw0413.
- Chen M, Zhang TL, Hu CG, Zhang JZ. 2023. The role of drought and temperature stress in the regulation of flowering time in annuals and perennials. *Agronomy* 13: 3034.

- Chen Y, Kaviani M, Najafabadi MY, McElroy M, Rajcan I, Navabi A. 2024. Copy number variation at *Vrn-A1* and haplotype diversity at *Fr-A2* are major determinants of winter survival of winter wheat (*Triticum aestivum* L.) in Eastern Canada. *Canadian Journal of Plant Science* 104: 336. doi:10.1139/cjps-2023-0101
- Chong K, Bao SL, Xu T, et al. 1998. Functional analysis of the *ver* gene using antisense transgenic wheat. *Physiologia Plantarum* 102: 87–92.
- Chow BY, Helfer A, Nusinow DA, Kay SA. 2012. *ELF3* recruitment to the *PRR9* promoter requires other Evening Complex members in the *Arabidopsis* circadian clock. *Plant Signaling and Behavior* 7: 170–173.
- Chu CG, Tan CT, Yu GT, Zhong S, Xu SS, Yan L. 2011. A novel retrotransposon inserted in the dominant *vrn-B1* allele confers spring growth habit in tetraploid wheat (*Triticum turgidum* L.). *G3 (Bethesda)* 1: 637–645.
- Cockram J, Jones H, Leigh FJ, et al. 2007. Control of flowering time in temperate cereals: genes, domestication, and sustainable productivity. *Journal of Experimental Botany* 58: 1231–1244.
- Covington MF, Panda S, Liu XL, Strayer CA, Wagner DR, Kay SA. 2001. *ELF3* modulates resetting of the circadian clock in *Arabidopsis*. *Plant Cell* 13: 1305–1315.
- Cseh A, Lenyók-Thegze A, Makai D, et al. 2024. Meiotic instability and irregular chromosome pairing underpin heat-induced infertility in bread wheat carrying the *Rht-B1b* or *Rht-D1b* Green Revolution genes. *The New Phytologist* 241: 180–196.
- Cui G, Li D, Zhang L, Xia C, Kong X, Liu X. 2023. *GSK3* regulates *VRN1* to control flowering time in wheat. *Journal of Integrative Plant Biology* 65: 1605–1608.
- Danyluk J, Kane NA, Breton G, Limin AE, Fowler DB, Sarhan F. 2003. *TaVRT-1*, a putative transcription factor associated with vegetative to reproductive transition in cereals. *Plant Physiology* 132: 1849–1860.
- Darko E, Heydarizadeh P, Schoefs B, Sabzalain MR. 2014. Photosynthesis under artificial light: the shift in primary and secondary metabolism. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 369: 20130243.
- Debernardi JM, Woods DP, Li K, Li C, Dubcovsky J. 2022. *MiR172-APETALA2*-like genes integrate vernalization and plant age to control flowering time in wheat. *PLoS Genetics* 18: e1010157.
- Del Río AR, Monteagudo A, Contreras-Moreira B, et al. 2023. Diversity of gene expression responses to light quality in barley. *Scientific Reports* 13: 17143.
- Deng W, Casao MC, Wang P, et al. 2015. Direct links between the vernalization response and other key traits of cereal crops. *Nature Communications* 6: 5882.
- Devlin PF, Patel SR, Whitelam GC. 1998. *Phytochrome E* influences internode elongation and flowering time in *Arabidopsis*. *The Plant Cell* 10: 1479–1487.
- Devlin PF, Robson PR, Patel SR, Goosey L, Sharrock RA, Whitelam GC. 1999. *Phytochrome D* acts in the shade-avoidance syndrome in *Arabidopsis* by controlling elongation growth and flowering time. *Plant Physiology* 119: 909–915.
- Diallo AO, Ali-Benali MA, Badawi M, Houde M, Sarhan F. 2012. Expression of vernalization responsive genes in wheat is associated with histone H3 trimethylation. *Molecular Genetics and Genomics* 287: 575–590.
- Díaz A, Zikhali M, Turner AS, Isaac P, Laurie DA. 2012. Copy number variation affecting the *Photoperiod-B1* and *Vernalization-A1* genes is associated with altered flowering time in wheat (*Triticum aestivum*). *PLoS One* 7: e33234.
- Distelfeld A, Dubcovsky J. 2010. Characterization of the maintained vegetative phase deletions from diploid wheat and their effect on *VRN2* and *FT* transcript levels. *Molecular Genetics and Genomics* 283: 223–232.
- Distelfeld A, Li C, Dubcovsky J. 2009a. Regulation of flowering in temperate cereals. *Current Opinion in Plant Biology* 12: 178–184.
- Distelfeld A, Tranquilli G, Li C, Yan L, Dubcovsky J. 2009b. Genetic and molecular characterization of the *VRN2* loci in tetraploid wheat. *Plant Physiology* 149: 245–257.
- Divashuk MG, Vasil'Ev AV, Bespalova LA, Karlov GI. 2012. Identity of the *Rht-11* and *Rht-B1e* reduced plant height genes. *Genetika* 48: 897–900.
- Dixon LE, Karsai I, Kiss T, et al. 2019. *VERNALIZATION1* controls developmental responses of winter wheat under high ambient temperatures. *Development* 146: dev172684.
- Dixon LE, Knox K, Kozma-Bognar L, Southern MM, Pokhilko A, Millar AJ. 2011. Temporal repression of core circadian genes is mediated through *EARLY FLOWERING 3* in *Arabidopsis*. *Current Biology: CB* 21: 120–125.
- Dixon LE, Farré A, Finnegan EJ, Orford S, Griffiths S, Boden SA. 2018. Developmental responses of bread wheat to changes in ambient temperature following deletion of a locus that includes *FLOWERING LOCUS T1*. *Plant, Cell and Environment* 41: 1715–1725.
- Dong H, Li D, Yang R, et al. 2023. *GSK3* phosphorylates and regulates the Green Revolution protein *Rht-B1b* to reduce plant height in wheat. *The Plant Cell* 35: 1970–1983.
- Dreccer MF, Wockner KB, Palta JA, et al. 2014. More fertile florets and grains per spike can be achieved at higher temperature in wheat lines with high spike biomass and sugar content at booting. *Functional Plant Biology* 41: 482–495.
- Dreisigacker S, Burgueño J, Pacheco A, et al. 2021. Effect of flowering time-related genes on biomass, harvest index, and grain yield in CIMMYT elite spring bread wheat. *Biology* 10: 855.
- Du Y, Chen L, Wang Y, et al. 2018. The combination of dwarfing genes *Rht4* and *Rht8* reduced plant height, improved yield traits of rainfed bread wheat (*Triticum aestivum* L.). *Field Crops Research* 215: 149–155.
- Dubcovsky J, Dvorak J. 2007. Genome plasticity a key factor in the success of polyploid wheat under domestication. *Science* 316: 1862–1866.
- Dubcovsky J, Lijavetzky D, Appendino L, Tranquilli G. 1998. Comparative RFLP mapping of *Triticum monoccoccum* genes controlling vernalization requirement. *Theoretical and Applied Genetics* 97: 968–975.
- Dubcovsky J, Loukoianov A, Fu D, Valarik M, Sanchez A, Yan L. 2006. Effect of photoperiod on the regulation of wheat vernalization genes *VRN1* and *VRN2*. *Plant Molecular Biology* 60: 469–480.
- Dubcovsky J, Li C, Distelfeld A, Pidal B, Tranquilli G. 2008. Genes and gene networks regulating wheat development. In: Appels R, Eastwood R, Lagudah E, Langridge P, Mackay M, McIntyre L, Sharp P. eds. *Proceedings of 11th International Wheat Genetics Symposium*. 25–29 August 2008, Brisbane: Sydney University Press.
- Efremova TT, Arbuzova VS, Leonova IN, Makhmudova K. 2011. Multiple allelism in the *Vrn-B1* locus of common wheat. *Cereal Research Communications* 39: 12–21.
- Ejaz M, von Korff M. 2017. The genetic control of reproductive development under high ambient temperature. *Plant Physiology* 173: 294–306.
- Ellis MH, Rebetzke GJ, Chandler P, Bonnett D, Spielmeier W, Richards RA. 2004. The effect of different height reducing genes on the early growth of wheat. *Functional Plant Biology* 31: 583–589.
- Ellis MH, Rebetzke GJ, Azanza F, Richards RA, Spielmeier W. 2005. Molecular mapping of gibberellin-responsive dwarfing genes in bread wheat. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* 111: 423–430.
- Eshed Y, Lippman ZB. 2019. Revolutions in agriculture chart a course for targeted breeding of old and new crops. *Science* 366: eaax0025.
- Faricelli ME, Valarik M, Dubcovsky J. 2016. Erratum to: Control of flowering time and spike development in cereals: the earliness *per se* *Eps-1* region in wheat, rice, and *Brachypodium*. *Functional and Integrative Genomics* 16: 593.
- Farre EM, Harmer SL, Harmon FG, Yanovsky MJ, Kay SA. 2005. Overlapping and distinct roles of *PRR7* and *PRR9* in the *Arabidopsis* circadian clock. *Current Biology: CB* 15: 47–54.
- Faure S, Turner AS, Gruszka D, et al. 2012. Mutation at the circadian clock gene *EARLY MATURITY 8* adapts domesticated barley (*Hordeum vulgare*) to short growing seasons. *Proceedings of the National Academy of Sciences of the United States of America* 109: 8328–8333.
- Febrer M, Wilhelm E, Al-Kaff N, et al. 2009. Rapid identification of the three homeologues of the wheat dwarfing gene *Rht* using a novel PCR-based screen of three-dimensional BAC pools. *Genome* 52: 993–1000.
- Feldman M. 1995. Wheats. In: Smartt J, Simmonds NW. eds. *Evolution of crop plants*. Harlow: Longman Scientific and Technical, 185–192.
- Fernández V, Takahashi Y, Le Gourrierc J, Coupland G. 2016. Photoperiodic and thermosensory pathways interact through *CONSTANS* to promote flowering at high temperature under short days. *The Plant Journal* 86: 426–440.
- Fernández-Calleja M, Casas AM, Igartua E. 2021. Major flowering time genes of barley: allelic diversity, effects, and comparison with wheat. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* 134: 1867–1897.
- Ferrándiz C, Gu Q, Martienssen R, Yanofsky MF. 2000. Redundant regulation of meristem identity and plant architecture by *FRUITFULL*, *APETALA1* and *CAULIFLOWER*. *Development* 127: 725–734.
- Findlay KM, Jenkins GI. 2016. Regulation of *UVR8* photoreceptor dimer/monomer photo-equilibrium in *Arabidopsis* plants grown under photoperiodic conditions. *Plant, Cell and Environment* 39: 1706–1714.

- Finnegan EJ, Ford B, Wallace X, *et al.* 2018. Zebularine treatment is associated with deletion of *FT-B1* leading to an increase in spikelet number in bread wheat. *Plant, Cell and Environment* **41**: 1346–1360.
- Fischer RA. 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. *The Journal of Agricultural Science* **105**: 447–461.
- Fjellheim S, Boden S, Trevaskis B. 2014. The role of seasonal flowering responses in adaptation of grasses to temperate climates. *Frontiers in Plant Science* **5**: 1–15.
- Flintham JE, Gale MD. 1983. The Tom Thumb dwarfing gene *Rht3* in wheat. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* **66**: 249–256.
- Flintham JE, Börner A, Worland AJ, Gale MD. 1997. Optimizing wheat grain yield, effects of *Rht* (gibberellin-insensitive) dwarfing genes. *The Journal of Agricultural Science* **128**: 11–25.
- Ford B, Deng W, Clausen J, *et al.* 2016. Barley (*Hordeum vulgare*) circadian clock genes can respond rapidly to temperature in an *EARLY FLOWERING* 3-dependent manner. *Journal of Experimental Botany* **67**: 5517–5528.
- Ford BA, Foo E, Sharwood R, *et al.* 2018. *Rht18* semidwarfism in wheat is due to increased *GA 2-oxidaseA9* expression and reduced GA content. *Plant Physiology* **177**: 168–180.
- Fornara F, De Montaigu A, Coupland G. 2010. SnapShot: control of flowering in *Arabidopsis*. *Cell* **141**: 550, 550.e1–550, 550.e2.
- Foulkes MJ, Sylvester-Bradley R, Worland AJ, Snape JW. 2004. Effect of a photoperiod response gene *Ppd-D1* on yield potential and drought resistance in UK winter wheat. *Euphytica* **135**: 63–73.
- Foulkes MJ, Slafer GA, Davies WJ, *et al.* 2011. Raising yield potential of wheat. III. Optimizing partitioning to grain while maintaining lodging resistance. *Journal of Experimental Botany* **62**: 469–486.
- Fowler S, Lee K, Onouchi H, *et al.* 1999. *GIGANTEA*: a circadian clock-controlled gene that regulates photoperiodic flowering in *Arabidopsis* and encodes a protein with several possible membrane-spanning domains. *The EMBO Journal* **18**: 4679–4688.
- Fowler SG, Cook D, Thomashow MF. 2005. Low temperature induction of *Arabidopsis* *CBF1*, 2, and 3 is gated by the circadian clock. *Plant Physiology* **137**: 961–968.
- Fu D, Szűcs P, Yan L, *et al.* 2005. Large deletions within the first intron in *VRN-1* are associated with spring growth habit in barley and wheat. *Molecular Genetics and Genomics* **273**: 54–65.
- Fu D, Dunbar M, Dubcovsky J. 2007. Wheat *VIN3-like* PHD finger genes are up-regulated by vernalization. *Molecular Genetics and Genomics* **277**: 301–313.
- Galiba G, Vágújfalvi A, Chengxia L, Soltész A, Dubcovsky J. 2009. Regulatory genes involved in the determination of frost tolerance in temperate cereals. *Plant Science* **176**: 12–19.
- Gao S, Chu C. 2020. Gibberellin metabolism and signaling: targets for improving agronomic performance of crops. *Plant and Cell Physiology* **61**: 1902–1911.
- García GA, Serrago RA, Appendino ML, *et al.* 2011. Variability of duration of preanthesis phases as a strategy for increasing wheat grain yield. *Field Crops Research* **124**: 408–416.
- Garner WW, Allard HA. 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *Monthly Weather Review* **48**: 415–415.
- Gauley A, Boden SA. 2021. Stepwise increases in *FT1* expression regulate seasonal progression of flowering in wheat (*Triticum aestivum*). *The New Phytologist* **229**: 1163–1176.
- Gauley A, Pasquariello M, Yoshikawa GV, *et al.* 2024. *Photoperiod-1* regulates the wheat inflorescence transcriptome to influence spikelet architecture and flowering time. *Current Biology* **34**: 2330–2343.e4.
- Gawroński P, Schnurbusch T. 2012. High-density mapping of the earliness per se-3A (*Eps-3A*) locus in diploid einkorn wheat and its relation to the syntenic regions in rice and *Brachypodium distachyon* L. *Molecular Breeding* **30**: 1097–1108.
- Gawroński P, Ariyadasa R, Himmelbach A, *et al.* 2014. A distorted circadian clock causes early flowering and temperature-dependent variation in spike development in the *Eps-3Am* mutant of einkorn wheat. *Genetics* **196**: 1253–1261.
- Golovnina KA, Kondratenko EY, Blinov AG, Goncharov NP. 2010. Molecular characterization of vernalization loci *VRN1* in wild and cultivated wheats. *BMC Plant Biology* **10**: 168.
- Goncharov NP. 1998. Genetic resources of wheat related species: The *Vrn* genes controlling growth habit (spring vs. winter). *Euphytica* **100**: 371–376.
- Goncharov NP. 2003. Genetics of growth habit (spring vs winter) in common wheat: confirmation of the existence of dominant gene *Vrn4*. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* **107**: 768–772.
- González FG, Slafer GA, Miralles DJ. 2002. Vernalization and photoperiod response in wheat pre-flowering reproductive phases. *Field Crops Research* **74**: 183–195.
- González FG, Slafer GA, Miralles DJ. 2003. Floret development, spike growth as affected by photoperiod during stem elongation in wheat. *Field Crops Research* **81**: 29–38.
- González FG, Slafer GA, Miralles DJ. 2005. Photoperiod during stem elongation in wheat: Is its impact on fertile floret and grain number determination similar to that of radiation? *Functional Plant Biology* **32**: 181–188.
- González-Navarro OE, Griffiths S, Molero G, Reynolds MP, Slafer GA. 2015. Dynamics of floret development determining differences in spike fertility in an elite population of wheat. *Field Crops Research* **172**: 21–31.
- González-Navarro OE, Griffiths S, Molero G, Reynolds MP, Slafer GA. 2016. Variation in developmental patterns among elite wheat lines and relationships with yield, yield components and spike fertility. *Field Crops Research* **196**: 294–304.
- Greenup A, Peacock WJ, Dennis ES, Trevaskis B. 2009. The molecular biology of seasonal flowering-responses in *Arabidopsis* and the cereals. *Annals of Botany* **103**: 1165–1172.
- Griffiths J, Murase K, Rieu I, *et al.* 2006. Genetic characterization and functional analysis of the *GID1* gibberellin receptors in *Arabidopsis*. *The Plant Cell* **18**: 3399–3414.
- Griffiths S, Simmonds J, Leverington M, *et al.* 2009. Meta-QTL analysis of the genetic control of ear emergence in elite European winter wheat germplasm. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* **119**: 383–395.
- Guo H, Yang H, Mockler TC, Liu C. 1998. Regulation of flowering time by *Arabidopsis* photoreceptors. *Science* **279**: 1360–1363.
- Guo Z, Chen D, Röder MS, Ganai MW, Schnurbusch T. 2018. Genetic dissection of pre-anthesis sub-phase durations during the reproductive spike development of wheat. *The Plant Journal* **95**: 909–918.
- Halliday KJ, Salter MG, Thingnaes E, Whitelam GC. 2003. Phytochrome control of flowering is temperature sensitive and correlates with expression of the floral integrator *FT*. *The Plant Journal: for Cell and Molecular Biology* **33**: 875–885.
- Halliwell J, Borrill P, Gordon A, *et al.* 2016. Systematic investigation of *FLOWERING LOCUS T*-like Poaceae gene families identifies the short-day expressed flowering pathway gene, *TaFT3* in wheat (*Triticum aestivum* L.). *Frontiers in Plant Science* **7**: 857.
- Hanocq E, Laperche A, Jaminon O, Lainé AL, Le Gouis J. 2007. Most significant genome regions involved in the control of earliness traits in bread wheat, as revealed by QTL meta-analysis. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* **114**: 569–584.
- Haque MA, Martinek P, Watanabe N, Kuboyama T. 2011. Genetic mapping of gibberellic acid-sensitive genes for semi dwarfism in durum wheat. *Cereal Research Communications* **39**: 171–178.
- Hazen SP, Schultz TF, Pruneda-Paz JL, Borevitz JO, Ecker JR, Kay SA. 2005. *LUX ARRHYTHMO* encodes a Myb domain protein essential for circadian rhythms. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 10387–10392.
- Helfer A, Nusinow DA, Chow BY, Gehrke AR, Bulyk ML, Kay SA. 2011. *LUX ARRHYTHMO* encodes a nighttime repressor of circadian gene expression in the *Arabidopsis* core clock. *Current Biology: CB* **21**: 126–133.
- Hemming MN, Peacock WJ, Dennis ES, Trevaskis B. 2008. Integration of seasonal flowering time responses in temperate cereals. *Plant Signaling and Behavior* **3**: 601–602.
- Hemming MN, Walford SA, Fieg S, Dennis ES, Trevaskis B. 2012. Identification of high temperature responsive genes in cereals. *Plant Physiology* **158**: 1439–1450.
- Herrero E, Kolmos E, Bujdoso N, *et al.* 2012. *EARLY FLOWERING4* recruitment of *EARLY FLOWERING3* in the nucleus sustains the *Arabidopsis* circadian clock. *The Plant Cell* **24**: 428–443.
- Herzig P, Maurer A, Draba V, *et al.* 2018. Contrasting genetic regulation of plant development in wild barley grown in two European environments revealed by nested association mapping. *Journal of Experimental Botany* **69**: 1517–1531.
- Higgins JA, Bailey PC, Laurie DA. 2010. Comparative genomics of flowering time pathways using *Brachypodium distachyon* as a model for the temperate grasses. *PLoS One* **5**: e10065.

- Hirano K, Asano K, Tsuji H, *et al.* 2010. Characterization of the molecular mechanism underlying gibberellin perception complex formation in rice. *The Plant Cell* **22**: 2680–2696.
- Hitz T, Hartung J, Graeff-Hoenninger S, Munz S. 2019. Morphological response of soybean (*Glycine max* (L.) Merr.) cultivars to light intensity and red to far-red ratio. *Agronomy* **9**: 428.
- Hoogendoorn J. 1985. A reciprocal F₁ monosomic analysis of the genetic control of time of ear emergence, number of leaves and number of spikelets in wheat (*Triticum aestivum* L.). *Euphytica* **34**: 545–558.
- Hoogendoorn J, Rickson JM, Gale MD. 1990. Differences in leaf and stem anatomy related to plant height of tall and dwarf wheat (*Triticum aestivum* L.). *Journal of Plant Physiology* **136**: 72–77.
- Horváth A, Kiss T, Berki Z, *et al.* 2023. Effects of the genetic components of plant development on yield related traits in wheat (*Triticum aestivum* L.) under non-stressed conditions. *Frontiers in Plant Science* **13**: 1070410.
- Hsu PY, Harmer SL. 2014. Wheels within wheels: the plant circadian system. *Trends in Plant Science* **19**: 240–249.
- Huang W, Perez-Garcia P, Pokhilko A, *et al.* 2012a. Mapping the core of the *Arabidopsis* circadian clock defines the network structure of the oscillator. *Science* **336**: 75–79.
- Huang Y, Yang W, Pei Z, *et al.* 2012b. The genes for gibberellin biosynthesis in wheat. *Functional and Integrative Genomics* **12**: 199–206.
- Huang Y, Kamal R, Shanmugaraj N, *et al.* 2023. A molecular framework for grain number determination in barley. *Science Advances* **9**: eadd0324.
- Huang Y, Maurer A, Giehl RFH, *et al.* 2024. Dynamic phytomeric growth contributes to local adaptation in barley. *Molecular Biology and Evolution* **41**: msae011.
- Hyles J, Bloomfield MT, Hunt JR, Trethowan RM, Trevaskis B. 2020. Phenology and related traits for wheat adaptation. *Heredity* **125**: 417–430.
- Ikeda A, Ueguchi-Tanaka M, Sonoda Y, *et al.* 2001. *Slender rice*, a constitutive gibberellin response mutant, is caused by a null mutation of the *SLR1* gene, an ortholog of the height-regulating gene *GAI/RGA/RHT/D8*. *The Plant Cell* **13**: 999–1010.
- Ito S, Song YH, Imaizumi T. 2012. LOV domain-containing F-box proteins: light-dependent protein degradation modules in *Arabidopsis*. *Molecular Plant* **5**: 573–582.
- Iuchi S, Suzuki H, Kim YC, *et al.* 2007. Multiple loss-of-function of *Arabidopsis* gibberellin receptor *AtGID1s* completely shuts down a gibberellin signal. *The Plant Journal: for Cell and Molecular Biology* **50**: 958–966.
- Ivaničová Z, Jakobson I, Reis D, *et al.* 2016. Characterization of new allele influencing flowering time in bread wheat introgressed from *Triticum militinae*. *New Biotechnology* **33**: 718–727.
- Iwaki K, Nishida J, Yanagisawa T, Yoshida H, Kato K. 2002. Genetic analysis of *vrn-B1* for vernalization requirement by using linked dCAPS markers in bread wheat (*Triticum aestivum* L.). *Theoretical and Applied Genetics* **104**: 571–576.
- 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.
- Jacott CN, Boden SA. 2020. Feeling the heat: developmental and molecular responses of wheat and barley to high ambient temperatures. *Journal of Experimental Botany* **71**: 5740–5751.
- James AB, Monreal JA, Nimmo GA, *et al.* 2008. The circadian clock in *Arabidopsis* roots is a simplified slave version of the clock in shoots. *Science* **322**: 1832–1835.
- Jiang C, Fu X. 2007. GA action: turning on de-DELLA repressing signaling. *Current Opinion in Plant Biology* **10**: 461–465.
- Johansson M, Staiger D. 2014. Time to flower: interplay between photoperiod and the circadian clock. *Journal of Experimental Botany* **66**: 719–730.
- Jones H, Leigh FJ, Mackay I, *et al.* 2008. Population-based resequencing reveals that the flowering time adaptation of cultivated barley originated east of the Ferile Crescent. *Molecular Biology and Evolution* **25**: 2211–2219.
- Jones HE, Lukac M, Brak B, *et al.* 2017. Photoperiod sensitivity affects flowering duration in wheat. *The Journal of Agricultural Science* **155**: 32–43.
- Jung JH, Domijan M, Klose C, *et al.* 2016. Phytochromes function as thermosensors in *Arabidopsis*. *Science* **354**: 886–889.
- Kamran A, Iqbal M, Spaner D. 2014. Flowering time in wheat (*Triticum aestivum* L.): a key factor for global adaptability. *Euphytica* **197**: 1–26.
- Kane NA, Danyluk J, Tardif G, *et al.* 2005. *TaVRT-2*, a member of the StMADS-11 clade of flowering repressors, is regulated by vernalization and photoperiod in wheat. *Plant Physiology* **138**: 2354–2363.
- Kane NA, Agharbaoui Z, Diallo AO, *et al.* 2007. *TaVRT2* represses transcription of the wheat vernalization gene *TaVRN1*. *The Plant Journal: for Cell and Molecular Biology* **51**: 670–680.
- Kardailsky I, Shukla VK, Ahn JH, *et al.* 1999. Activation tagging of the floral inducer *FT*. *Science* **286**: 1962–1965.
- Karsai I, Mészáros K, Hayes PM, Bedő Z. 1997. Effects of loci on chromosomes 2(2H) and 7(5H) on developmental patterns in barley (*Hordeum vulgare* L.) under different photoperiod regimes. *Theoretical and Applied Genetics* **94**: 612–618.
- Karsai I, Szűcs P, Mészáros K, *et al.* 2005. The *Vrn-H2* locus is a major determinant of flowering time in a facultative winter growth habit barley (*Hordeum vulgare* L.) mapping population. *Theoretical and Applied Genetics* **110**: 1458–1466.
- Karsai I, Mészáros K, Szűcs P, Hayes PM, Láng L, Bedő Z. 2006. The *Vrn-H2* locus (4H) is influenced by photoperiod and is a major determinant of plant development and reproductive fitness traits in a facultative × winter barley (*Hordeum vulgare* L.) mapping population. *Plant Breeding* **125**: 468–472.
- Karsai I, Szűcs P, Kőszegi B, *et al.* 2008. Effects of photo and thermo cycles on flowering time in barley: a genetical phenomics approach. *Journal of Experimental Botany* **59**: 2707–2715.
- Karsai I, Igartua E, Casas AM, *et al.* 2013. Developmental patterns of a large set of barley (*Hordeum vulgare*) cultivars in response to ambient temperature. *Annals of Applied Biology* **162**: 309–323.
- Kato K, Wada T. 1999. Genetic analysis and selection experiment for narrow-sense earliness in wheat by using segregating hybrid progenies. *Breeding Science* **49**: 233–238.
- Kato K, Miura H, Sawada S. 2000. Mapping QTLs controlling grain yield and its components on chromosome 5A of wheat. *Theoretical and Applied Genetics* **101**: 1114–1121.
- Kato H, Taketa S, Ban T, Iriki N, Murai K. 2001. The influence of a spring habit gene, *Vrn-D1*, on heading time in wheat. *Plant Breeding* **120**: 115–120.
- Keyes GJ, Paolillo DJ, Sorrells ME. 1989. The effects of dwarfing genes *Rht1* and *Rht2* on cellular dimensions and rate of leaf elongation in wheat. *Annals of Botany* **64**: 683–690.
- Khlestkina EK, Kumar U, Röder MS. 2010. Ent-kaurenoic acid oxidase genes in wheat. *Molecular Breeding* **25**: 251–258.
- Kim WY, Fujiwara S, Suh SS, *et al.* 2007. *ZEITLUPE* is a circadian photoreceptor stabilized by *GIGANTEA* in blue light. *Nature* **449**: 356–360.
- Kim DH, Doyle MR, Sung S, Amasino RM. 2009. Vernalization: winter and the timing of flowering in plants. *Annual Review of Cell and Developmental Biology* **25**: 277–299.
- Kim JJ, Lee JH, Kim W, Jung HS, Huijser P, Ahn JH. 2012. The microRNA 156-*SQUAMOSA* PROMOTER BINDING PROTEIN-LIKE3 module regulates ambient temperature-responsive flowering via *FLOWERING LOCUS T* in *Arabidopsis*. *Plant Physiology* **159**: 461–478.
- Kippes N, Zhu J, Chen A, *et al.* 2014. Fine mapping and epistatic interactions of the vernalization gene *VRN-D4* in hexaploid wheat. *Molecular Genetics and Genomics* **289**: 47–62.
- Kippes N, Debernardi JM, Vasquez-Gross HA, *et al.* 2015. Identification of the *VERNALIZATION 4* gene reveals the origin of spring growth habit in ancient wheats from South Asia. *Proceedings of the National Academy of Sciences of the United States of America* **112**: 5401–5410.
- Kippes N, Chen A, Zhang X, Lukaszewski AJ, Dubcovsky J. 2016. Development and characterization of a spring hexaploid wheat line with no functional *VRN2* genes. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* **129**: 1417–1428.
- Kippes N, Guedira M, Lin L, Alvarez MA, Brown-Guedira GL, Dubcovsky J. 2018. Single nucleotide polymorphisms in a regulatory site of *VRN-A1* first intron are associated with differences in vernalization requirement in winter wheat. *Molecular Genetics and Genomics* **293**: 1231–1243.
- Kirby EJM. 1988. Analysis of leaf, stem and ear growth in wheat from terminal spikelet stage to anthesis. *Field Crops Research* **18**: 127–140.
- Kiseleva AA, Salina EA. 2018. Genetic regulation of common wheat heading time. *Russian Journal of Genetics* **54**: 375–388.
- Kiseleva AA, Bragina MK, Muterko AF, Salina EA. 2022. Functional characterization of genes with daily expression patterns in common wheat. *Plant Molecular Biology* **109**: 135–146.
- Kiss T, Balla K, Veisz O, Karsai I. 2011. Elaboration of a non-destructive methodology for establishing plant developmental patterns in cereals. *Acta Agronomica Hungarica* **59**: 293–301.

- Kiss T, Balla K, Bányai J, Veisz O, Karsai I. 2014a. Effect of different sowing times on the plant developmental parameters of wheat (*Triticum aestivum* L.). *Cereal Research Communications* **42**: 239–251.
- Kiss T, Balla K, Veisz O, et al. 2014b. Allele frequencies in the *VRN-A1*, *VRN-B1* and *VRN-D1* vernalization response and *PPDB1* and *PPD-D1* photoperiod sensitivity genes, and their effects on heading in a diverse set of wheat cultivars (*Triticum aestivum* L.). *Molecular Breeding* **34**: 297–310.
- Kiss T, Dixon LE, Soltész A, et al. 2017. Effects of ambient temperature in association with photoperiod on phenology and on the expressions of major plant developmental genes in wheat (*Triticum aestivum* L.). *Plant, Cell and Environment* **40**: 1629–1642.
- Kiss T, Bányai J, Balla K, et al. 2019. Comparative study of the developmental traits and yield components of bread wheat under field conditions in several years of multi-sowing time experiments. *Crop Science* **59**: 591–604.
- 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 and Genetic Systems* **87**: 161–168.
- Kobayashi Y, Kaya H, Goto K, Iwabuchi M, Araki T. 1999. A pair of related genes with antagonistic roles in mediating flowering signals. *Science* **286**: 1960–1962.
- Kolmos E, Nowak M, Werner M, et al. 2009. Integrating *ELF4* into the circadian system through combined structural and functional studies. *HFSP Journal* **3**: 350–366.
- Komeda Y. 2004. Genetic regulation of time to flower in *Arabidopsis thaliana*. *Annual Review of Plant Biology* **55**: 521–535.
- Kong Y, Zheng Y. 2020. Phototropin is partly involved in blue-light-mediated stem elongation, flower initiation, and leaf expansion: a comparison of phenotypic responses between wild *Arabidopsis* and its phototropin mutants. *Environmental and Experimental Botany* **171**: 103967.
- Konzak CF. 1987. Mutations and mutation breeding. In: Heyne EC. ed. *Wheat and wheat improvement*, 2nd edn. Madison, WI: American Society of Agronomy, 428–443.
- Kronenberg L, Yates S, Boer MP, Kirchgessner N, Walter A, Hund A. 2021. Temperature response of wheat affects final height and the timing of stem elongation under field conditions. *Journal of Experimental Botany* **72**: 700–717.
- Kumar S, Sharma V, Chaudhary S, et al. 2012. Genetics of flowering time in bread wheat *Triticum aestivum*: complementary interaction between vernalization-insensitive and photoperiod-insensitive mutations imparts very early flowering habit to spring wheat. *Journal of Genetics* **91**: 33–47.
- Kurepin LV, Yip WK, Fan R, Yeung EC, Reid DM. 2010. The roles and interactions of ethylene with gibberellins in the far-red enriched light-mediated growth of *Solanum lycopersicum* seedlings. *Plant Growth Regulation* **61**: 215–222.
- Langer SM, Longin CFH, Würschum T. 2014. Flowering time control in European winter wheat. *Frontiers in Plant Science* **5**: 537.
- Laurie DA. 1997. Comparative genetics of flowering time. *Plant Molecular Biology* **35**: 167–177.
- Laurie DA, Pratchett N, Bezant JH, Snape JW. 1995. RFLP mapping of five major genes and eight quantitative trait loci controlling flowering time in a winter × spring barley *Hordeum vulgare* L. cross. *Genome* **38**: 575–585.
- Law CN, Worland AJ, Giorgi B. 1976. The genetic control of ear emergence time by chromosomes 5A and 5D of wheat. *Heredity* **36**: 49–58.
- Law CN, Sutka J, Worland AJ. 1978. A genetic study of daylength response in wheat. *Heredity* **41**: 185–191.
- Lazaro A, Mouriz A, Pineiro M, Jarillo JA. 2015. Red light-mediated degradation of *CONSTANS* by the E3 ubiquitin ligase *HOS1* regulates photoperiodic flowering in *Arabidopsis*. *The Plant Cell* **27**: 2437–2454.
- Legris M, Klose C, Burgie ES, et al. 2016. Phytochrome B integrates light and temperature signals in *Arabidopsis*. *Science* **354**: 897–900.
- Levy YY, Dean C. 1998. The transition to flowering. *The Plant Cell* **10**: 1973–1990.
- Lewis S, Faricelli ME, Appendino ML, Valárik M, Dubcovsky J. 2008. The chromosome region including the earliness per se locus *Eps-Am1* affects the duration of early developmental phases and spikelet number in diploid wheat. *Journal of Experimental Botany* **59**: 3595–3607.
- Li C, Dubcovsky J. 2008. Wheat FT protein regulates *VRN1* transcription through interactions with FDL2. *The Plant Journal: for Cell and Molecular Biology* **55**: 543–554.
- Li J, Li Y, Chen S, An L. 2010. Involvement of brassinosteroid signals in the floral-induction network of *Arabidopsis*. *Journal of Experimental Botany* **61**: 4221–4230.
- Li C, Distelfeld A, Comis A, Dubcovsky J. 2011. Wheat flowering repressor *VRN2* and promoter *CO2* compete for interactions with *NUCLEAR FACTOR-Y* complexes. *The Plant Journal: for Cell and Molecular Biology* **67**: 763–773.
- Li YY, Xiao JH, Wu JJ, et al. 2012. A tandem segmental duplication (TSD) in green revolution gene *Rht-D1b* region underlies plant height variation. *The New Phytologist* **196**: 282–291.
- Li A, Liu D, Wu J, et al. 2014. mRNA and small RNA transcriptomes reveal insights into dynamic homeolog regulation of allopolyploid heterosis in nascent hexaploid wheat. *The Plant Cell* **26**: 1878–1900.
- Li Q, Byrns B, Badawi MY, et al. 2018. Transcriptomic insights into phenological development and cold tolerance of wheat grown in the field. *Plant Physiology* **176**: 2376–2394.
- Li C, Lin H, Debernardi JM, Zhang C, Dubcovsky J. 2024. *GIGANTEA* accelerates wheat heading time through gene interactions converging on *FLOWERING LOCUS T1*. *The Plant Journal: for Cell and Molecular Biology* **118**: 519–533.
- Lin X, Fang C, Liu B, Kong F. 2021. Natural variation and artificial selection of photoperiodic flowering genes and their applications in crop adaptation. *ABIOTECH* **2**: 156–169.
- Liu H, Liu B, Zhao C, Pepper M, Lin C. 2011. The action mechanisms of plant cryptochromes. *Trends in Plant Science* **16**: 684–691.
- Liu X, Zheng S, Tian S, et al. 2024. Natural variant of *Rht27*, a dwarfing gene, enhances yield potential in wheat. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* **137**: 128.
- Llanes A, Andrade A, Masciarelli O, Alemanno S, Luna V. 2016. Drought and salinity alter endogenous hormonal profiles at the seed germination phase. *Seed Science Research* **26**: 1–13.
- Loskutova NP. 1998. The influence of *Rht1-5*, *Rht8-9* and *Rht13* genes on morphological characters and yield productivity of wheat. In: Slinkard AE. ed. *Proceedings of the 9th International Wheat Genetics Symposium*. Saskatoon: University Extension Press. University Saskatchewan, 283–284.
- Loukoianov A, Yan L, Blechl A, Sanchez A, Dubcovsky J. 2005. Regulation of *VRN-1* vernalization response genes in normal and transgenic polyploid wheat. *Plant Physiology* **138**: 2364–2373.
- Lu Y, Xing L, Xing S, et al. 2015. Characterization of a putative new semi-dominant reduced height gene, *Rht-NM9*, in wheat (*Triticum aestivum* L.). *Journal of Genetics and Genomics = Yi Chuan Xue Bao* **42**: 685–698.
- Luo X, Liu B, Xie L, et al. 2024. The *TaSOC1-TaVRN1* module integrates photoperiod and vernalization signals to regulate wheat flowering. *Plant Biotechnology Journal* **22**: 635–649.
- Lv B, Nitcher R, Han X, et al. 2014. Characterization of *FLOWERING LOCUS T1 (FT1)* gene in *Brachypodium* and wheat. *PLoS One* **9**: e94171.
- MacMillan CP, Blundell CA, King RW. 2005. Flowering of the grass *Lolium perenne*. Effects of vernalization and long days on gibberellin biosynthesis and signaling. *Plant Physiology* **138**: 1794–1806.
- Makhoul M, Chawla HS, Wittkop B, et al. 2022. Long-amplicon single-molecule sequencing reveals novel, trait-associated variants of *VERNALIZATION1* homeologs in hexaploid wheat. *Frontiers in Plant Science* **13**: 942461.
- Makhoul M, Schlichtermann RH, Ugwuanyi S, et al. 2024. Novel *PHOTOPERIOD-1* gene variants associate with yield-related and root-angle traits in European bread wheat. *Theoretical and Applied Genetics* **137**: 125.
- Mandel MA, Yanofsky MF. 1995. A gene triggering flower formation in *Arabidopsis*. *Nature* **377**: 522–524.
- Matsushika A, Makino S, Kojima M, Mizuno T. 2000. Circadian waves of expression of the *APRR1/TOC1* family of pseudo-response regulators in *Arabidopsis thaliana*: insight into the plant circadian clock. *Plant and Cell Physiology* **41**: 1002–1012.
- Maurer A, Draba V, Pillen K. 2016. Genomic dissection of plant development and its impact on thousand grain weight in barley through nested association mapping. *Journal of Experimental Botany* **67**: 2507–2518.
- Mazzella MA, Casal JJ. 2001. Interactive signalling by phytochromes and cryptochromes generates de-etiolation homeostasis in *Arabidopsis thaliana*. *Plant, Cell and Environment* **24**: 155–161.
- McClung CR. 2006. Plant circadian rhythms. *The Plant Cell* **18**: 792–803.
- McClung CR. 2021. Circadian clock components offer targets for crop domestication and improvement. *Genes* **12**: 374.
- McIntosh RA, Yamazaki Y, Devos KM, Dubcovsky J, Rogers WJ, Appels R. 2003. Catalogue of gene symbols for wheat. In: McIntosh RA, Pogna

- NE. ed. *Tenth International Wheat Genetics Symposium: Proceedings*. Rome: Istituto Sperimentale per la Cerealicoltura, 1–47.
- McKim SM. 2020. Moving on up—controlling internode growth. *New Phytologist* **226**: 672–678.
- McMaster GS. 2005. Phytomers, phyllochrons, phenology and temperate cereal development. *The Journal of Agricultural Science* **143**: 137–150.
- Milec Z, Tomková L, Sumíková T, Pánková K. 2012. A new multiplex PCR test for the determination of *vrn-B1* alleles in bread wheat (*Triticum aestivum* L.). *Molecular Breeding* **30**: 317–323.
- Milec Z, Sumikova T, Tomkova L, Pankova K. 2013. Distribution of different *Vrn-B1* alleles in hexaploid spring wheat germplasm. *Euphytica* **192**: 371–378.
- Milec Z, Strejčková B, Šafář J. 2023. Contemplation on wheat vernalization. *Frontiers in Plant Science* **13**: 1093792.
- Miralles DJ, Richards RA. 2000. Responses of leaf and tiller emergence and primordium initiation in wheat and barley to interchanged photoperiod. *Annals of Botany* **85**: 655–663.
- Miralles DJ, Richards RA, Slafer GA. 2000. Duration of stem elongation period influences the number of fertile florets in wheat, barley. *Australian Journal of Plant Physiology* **27**: 931–940.
- Mizuno T, Nakamichi N. 2005. Pseudo-response regulators (PRRs) or true oscillator components (TOCs). *Plant and Cell Physiology* **46**: 677–685.
- Mizuno N, Nitta M, Sato K, Nasuda S. 2012. A wheat homologue of *PHYTOCLOCK 1* is a candidate gene conferring the early heading phenotype to einkorn wheat. *Genes and Genetic Systems* **87**: 357–367.
- Mizuno N, Kinoshita M, Kinoshita S, et al. 2016. Loss-of-function mutations in three homoeologous *PHYTOCLOCK 1* genes in common wheat are associated with the extra-early flowering phenotype. *PLoS One* **11**: e0165618.
- Mo Y, Vanzetti LS, Hale I, et al. 2018. Identification and characterization of *Rht25*, a locus on chromosome arm 6AS affecting wheat plant height, heading time, and spike development. *Theoretical and Applied Genetics* **131**: 2021–2035.
- Mohan A, Grant NP, Schillinger WF, Gill KS. 2021. Characterizing reduced height wheat mutants for traits affecting abiotic stress and photosynthesis during seedling growth. *Physiologia Plantarum* **172**: 233–246.
- Monte E, Alonso JM, Ecker JR, et al. 2003. Isolation and characterization of *phyC* mutants in *Arabidopsis* reveals complex crosstalk between phytochrome signaling pathways. *The Plant Cell* **15**: 1962–1980.
- Monteagudo A, Kiss T, Mayer M, Casas AM, Igartua E, Karsai I. 2020. Genetic diversity in developmental responses to light spectral quality in barley (*Hordeum vulgare* L.). *BMC Plant Biology* **20**: 207.
- Morgan DC, Smith H. 1981. Non-photosynthetic responses to light quality. In: Lange OL, Nobel PS, Osmond CB, Ziegler H. eds. *Physiological plant ecology I. Responses to the physical environment*. Berlin: Springer, 109–134.
- Mouradov A, Cremer F, Coupland G. 2002. Control of flowering time: Interacting pathways as a basis for diversity. *The Plant Cell* **14**: S111–S130.
- Mulki MA, von Korff M. 2016. *CONSTANS* controls floral repression by up-regulating *VERNALIZATION2* (*VRN-H2*) in barley. *Plant Physiology* **170**: 325–337.
- Murai K, Miyamae M, Kato H, Takumi S, Ogihara Y. 2003. *WAP1*, a wheat *APETALA1* homolog, plays a central role in the phase transition from vegetative to reproductive growth. *Plant and Cell Physiology* **44**: 1255–1265.
- Murase K, Hirano Y, Sun TP, Hakoshima T. 2008. Gibberellin-induced DELLA recognition by the gibberellin receptor GID1. *Nature* **456**: 459–463.
- Mutasa-Göttgens E, Hedden P. 2009. Gibberellin as a factor in floral regulatory networks. *Journal of Experimental Botany* **60**: 1979–1989.
- Muterko AF, Salina E. 2017. Analysis of the *VERNALIZATION-A1* exon-4 polymorphism in polyploid wheat. *Vavilov Journal of Genetics and Breeding* **21**: 323–333.
- Muterko A, Salina E. 2019. *VRN1*-ratio test for polyploid wheat. *Planta* **250**: 1955–1965.
- Muterko A, Salina E. 2021. Features of transcriptional dynamics of the duplicated *Vernalization-B1* gene in wheat (*Triticum* spp.). *Plant Breeding* **140**: 1023–1031.
- Muterko A, Balashova I, Cockram J, Kalendar R, Sivolap Y. 2015. The new wheat vernalization response allele *vrn-D1s* is caused by DNA transposon insertion in the first intron. *Plant Molecular Biology Reporter* **33**: 294–303.
- Muterko A, Kalendar R, Salina E. 2016. Novel alleles of the *VERNALIZATION1* genes in wheat are associated with modulation of DNA curvature and flexibility in the promoter region. *BMC Plant Biology* **16**: 65–81.
- Nakajima M, Shimada A, Takashi Y, et al. 2006. Identification and characterization of *Arabidopsis* gibberellin receptors. *The Plant Journal: for Cell and Molecular Biology* **46**: 880–889.
- Nishida H, Ishihara D, Ishii M, et al. 2013a. Phytochrome C is a key factor controlling long-day flowering in barley. *Plant Physiology* **163**: 804–814.
- Nishida H, Yoshida T, Kawakami K, et al. 2013b. Structural variation in the 5' upstream region of photoperiod-insensitive alleles *Ppd-A1a* and *Ppd-B1a* identified in hexaploid wheat (*Triticum aestivum* L.), and their effect on heading time. *Molecular Breeding* **31**: 27–37.
- Nishimura K, Handa H, Mori N, Kawaura K, Kitajima A, Nakazaki T. 2021. Geographical distribution and adaptive variation of *VRN-A3* alleles in worldwide polyploid wheat (*Triticum* spp.) species collection. *Planta* **253**: 1–14.
- Nishiura A, Kazama Y, Abe T, Mizuno N, Nasuda S, Murai K. 2014. Level of *VERNALIZATION 1* expression is correlated with earliness in extra early-flowering mutant wheat lines. *Breeding Science* **64**: 213–221.
- Nishiura A, Kitagawa S, Matsumura M, et al. 2018. An early-flowering einkorn wheat mutant with deletions of *PHYTOCLOCK 1/LUX ARRHYTHMO* and *VERNALIZATION 2* exhibits a high level of *VERNALIZATION 1* expression induced by vernalization. *Journal of Plant Physiology* **222**: 28–38.
- Nitcher R, Distelfeld A, Tan C, Yan L, Dubcovsky J. 2013. Increased copy number at the *HvFT1* locus is associated with accelerated flowering time in barley. *Molecular Genetics and Genomics* **288**: 261–275.
- Ochagavía H, Prieto P, Savin R, Griffiths S, Slafer GA. 2018. Earliness *per se* effects on developmental traits in hexaploid wheat grown under field conditions. *European Journal of Agronomy* **99**: 214–223.
- Ochagavía H, Prieto P, Zikhali M, Griffiths S, Slafer GA. 2019. Earliness *per se* by temperature interaction on wheat development. *Scientific Reports* **9**: 2584.
- Oliver SN, Finnegan EJ, Dennis ES, Peacock WJ, Trevaskis B. 2009. Vernalization-induced flowering in cereals is associated with changes in histone methylation at the *VERNALIZATION1* gene. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 8386–8391.
- Olszewski N, Sun TP, Gubler F. 2002. Gibberellin signaling: biosynthesis, catabolism, and response pathways. *The Plant Cell* **14**: S61–S80.
- Pankin A, Campoli C, Dong X, et al. 2014. Mapping-by-sequencing identifies *HvPHYTOCHROME C* as a candidate gene for the *early maturity 5* locus modulating the circadian clock and photoperiodic flowering in barley. *Genetics* **198**: 383–396.
- Parrado JD, Savin R, Slafer GA. 2023. Photoperiod sensitivity of *Ppd-H1* and *ppd-H1* isogenic lines of a spring barley cultivar: exploring extreme photoperiods. *Journal of Experimental Botany* **74**: 6608–6618.
- Pearce S, Vanzetti LS, Dubcovsky J. 2013. Exogenous gibberellins induce wheat spike development under short days only in the presence of *VERNALIZATION1*. *Plant Physiology* **163**: 1433–1445.
- Pearce S, Kippes N, Chen A, Debernardi JM, Dubcovsky J. 2016. RNA-seq studies using wheat *PHYTOCHROME B* and *PHYTOCHROME C* mutants reveal shared and specific functions in the regulation of flowering and shade-avoidance pathways. *BMC Plant Biology* **16**: 141.
- Peng J, Carol P, Richards DE, et al. 1997. The *Arabidopsis* *GAI* gene defines a signaling pathway that negatively regulates gibberellin responses. *Genes and Development* **11**: 3194–3205.
- Peng J, Richards DE, Hartley NM, et al. 1999. 'Green revolution' genes encode mutant gibberellin response modulators. *Nature* **400**: 256–261.
- Peng ZS, Li X, Yang ZJ, Liao ML. 2011. A new reduced height gene found in the tetraploid semi-dwarf wheat landrace Aiganfanmai. *Genetics and Molecular Research: GMR* **10**: 2349–2357.
- Peng FY, Hu Z, Yang R. 2015. Genome-wide comparative analysis of flowering-related genes in *Arabidopsis*, wheat, and barley. *International Journal of Plant Genomics* **2015**: 874361.
- Perez-Gianmarco TI, Slafer GA, Gonzalez FG. 2019. Photoperiod-sensitivity genes shape floret development in wheat. *Journal of Experimental Botany* **70**: 1339–1348.
- Pham VN, Kathare PK, Huq E. 2018. Phytochromes and phytochrome interacting factors. *Plant Physiology* **176**: 1025–1038.

- Pieper R, Tomé F, Pankin A, von Korff M. 2021. *FLOWERING LOCUS T4* delays flowering and decreases floret fertility in barley. *Journal of Experimental Botany* 72: 107–121.
- Porter JR, Gawith M. 1999. Temperatures and the growth and development of wheat: a review. *European Journal of Agronomy* 10: 23–36.
- Porter JR, Semenov MA. 2005. Crop responses to climatic variation. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 360: 2021–2035.
- Preston JC, Kellogg EA. 2008. Discrete developmental roles for temperate cereal grass *VERNALIZATION1/FRUITFULL*-like genes in flowering competency and the transition to flowering. *Plant Physiology* 146: 265–276.
- Prieto P, Ochagavía H, Savin R, Griffiths S, Slafer GA. 2018a. Dynamics of floret initiation/death determining spike fertility in wheat as affected by *Ppd* genes under field conditions. *Journal of Experimental Botany* 69: 2633–2645.
- Prieto P, Ochagavía H, Savin R, Griffiths S, Slafer GA. 2018b. Physiological determinants of fertile floret survival in wheat as affected by earliness per se genes under field conditions. *European Journal of Agronomy* 99: 206–213.
- Prieto P, Ochagavía H, Griffiths S, Slafer GA. 2020. Earliness per se × temperature interaction: consequences on leaf, spikelet, and floret development in wheat. *Journal of Experimental Botany* 71: 1956–1968.
- Pugsley AT. 1966. The photoperiodic sensitivity of some spring wheats with special reference to the variety Thatcher. *Australian Journal of Agricultural Research* 17: 591–599.
- Pugsley AT. 1971. A genetic analysis of the spring-winter habit of growth in wheat. *Australian Journal of Agricultural Research* 22: 21–23.
- Pugsley AT. 1972. Additional genes inhibiting winter habit in wheat. *Euphytica* 21: 547–552.
- Quiroz S, Yustis JC, Chávez-Hernández EC, et al. 2021. Beyond the genetic pathways, flowering regulation complexity in *Arabidopsis thaliana*. *International Journal of Molecular Sciences* 22: 5716.
- Rawson HM, Richards RA. 1993. Effects of high temperature and photoperiod on floral development in wheat isolines differing in vernalisation and photoperiod genes. *Field Crops Research* 32: 181–192.
- Rees H, Rusholme-Pilcher R, Bailey P, et al. 2022. Circadian regulation of the transcriptome in a complex polyploid crop. *PLoS Biology* 20: e3001802.
- Rehman S, Bahadur S, Xia W. 2023. An overview of floral regulatory genes in annual and perennial plants. *Gene* 885: 147699.
- Reynolds M, Foulkes MJ, Slafer GA, et al. 2009. Raising yield potential in wheat. *Journal of Experimental Botany* 60: 1899–1918.
- Roberts EH, Summerfield RJ, Cooper JP, Ellis RH. 1988. Environmental control of flowering in barley (*Hordeum vulgare* L.). I. Photoperiod limits to long-day responses, photoperiod-insensitive phases and effects of low-temperature and short-day vernalization. *Annals of Botany* 62: 127–144.
- Salome PA, McClung CR. 2005. *PSEUDO-RESPONSE REGULATOR 7* and *9* are partially redundant genes essential for the temperature responsiveness of the *Arabidopsis* circadian clock. *The Plant Cell* 17: 791–803.
- Samach A, Wigge PA. 2005. Ambient temperature perception in plants. *Current Opinion in Plant Biology* 8: 483–486.
- Samach A, Onouchi H, Gold SE, et al. 2000. Distinct roles of *CONSTANS* target genes in reproductive development of *Arabidopsis*. *Science* 288: 1613–1616.
- Sanchez SE, Rugnone ML, Kay SA. 2020. Light perception: a matter of time. *Molecular Plant* 13: 363–385.
- Santra DK, Santra M, Allan RE, Campbell KG, Kidwell KK. 2009. Genetic and molecular characterization of vernalization genes *vrn-A1*, *vrn-B1*, and *vrn-D1* in spring wheat germplasm from the Pacific Northwest region of the U.S.A. *Plant Breeding* 128: 576–584.
- Sawa M, Nusinow DA, Kay SA, Imaizumi T. 2007. *FKF1* and *GIGANTEA* complex formation is required for day-length measurement in *Arabidopsis*. *Science* 318: 261–265.
- Scarth R, Law CN. 1984. The control of the day-length response in wheat by the group 2 chromosomes. *Zeitschrift für Pflanzenzüchtung* 92: 140–150.
- Schaffer R, Ramsay N, Samach A, et al. 1998. The late elongated hypocotyl mutation of *Arabidopsis* disrupts circadian rhythms and the photoperiodic control of flowering. *Cell* 93: 1219–1229.
- Schultz TF, Kiyosue T, Yanovsky M, Wada M, Kay SA. 2001. A role for *LKP2* in the circadian clock of *Arabidopsis*. *The Plant Cell* 13: 2659–2670.
- Shaw LM, Turner AS, Laurie DA. 2012. The impact of photoperiod insensitive *Ppd-1a* mutations on the photoperiod pathway across the three genomes of hexaploid wheat (*Triticum aestivum*). *The Plant Journal: for Cell and Molecular Biology* 71: 71–84.
- 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.
- Shaw LM, Lyu B, Turner R, et al. 2019. *FLOWERING LOCUS T2* regulates spike development and fertility in temperate cereals. *Journal of Experimental Botany* 70: 193–204.
- Shaw LM, Li CX, Woods DP, et al. 2020. Epistatic interactions between *PHOTOPERIOD1*, *CONSTANS1* and *CONSTANS2* modulate the photoperiodic response in wheat. *PLoS Genetics* 16: e1008812.
- Shcherban AB, Efremova TT, Salina EA. 2012. Identification of a new *vrn-B1* allele using two near-isogenic wheat lines with difference in heading time. *Molecular Breeding* 29: 675–685.
- Shcherban AB, Strygina KV, Salina EA. 2015. *VRN-1* gene-associated prerequisites of spring growth habit in wild tetraploid wheat *T. dicoccoides* and the diploid A genome species. *BMC Plant Biology* 15: 94.
- Shcherban AB, Schichkina AA, Salina EA. 2016. The occurrence of spring forms in tetraploid *Timopheevi* wheat is associated with variation in the first intron of the *VRN-A1* gene. *BMC Plant Biology* 16: 236.
- Sheldon CC, Rouse DT, Finnegan EJ, Peacock WJ, Dennis ES. 2000. The molecular basis of vernalization: the central role of *FLOWERING LOCUS C (FLC)*. *Proceedings of the National Academy of Sciences of the United States of America* 97: 3753–3758.
- Shewry PR, Hey SJ. 2015. The contribution of wheat to human diet and health. *Food and Energy Security* 4: 178–202.
- Shi C, Zhao L, Zhang X, Lv G, Pan Y, Chen F. 2019. Gene regulatory network and abundant genetic variation play critical roles in heading stage of polyploidy wheat. *BMC Plant Biology* 19: 6.
- Shimada S, Ogawa T, Kitagawa S, et al. 2009. A genetic network of flowering time genes in wheat leaves, in which an *APETALA1/FRUITFULL*-like gene, *VRN1*, is upstream of *FLOWERING LOCUS T*. *The Plant Journal* 58: 668–681.
- Shindo C, Sasakuma T, Watanabe N, Noda K. 2002. Two-gene systems of vernalization requirement and narrow-sense earliness in einkorn wheat. *Genome* 45: 563–569.
- Shitsukawa N, Ikari C, Mitsuya T, et al. 2007a. Wheat *SOC1* functions independently of *WAP1/VRN1*, an integrator of vernalization and photoperiod flowering promotion pathways. *Physiologia Plantarum* 130: 627–636.
- Shitsukawa N, Ikari C, Shimada S, et al. 2007b. The einkorn wheat (*Triticum monococcum*) mutant, maintained vegetative phase, is caused by a deletion in the *VRN1* gene. *Genes and Genetic System* 82: 167–170.
- Slafer GA, Rawson HM. 1994. Sensitivity of wheat phasic development to major environmental factors: a re-examination of some assumptions made by physiologists and modellers. *Functional Plant Biology* 21: 393–426.
- Slafer GA, Rawson HM. 1995. Base and optimum temperatures vary with genotype and stage of development in wheat. *Plant, Cell & Environment* 18: 671–679.
- Slafer GA, Rawson HM. 1996. Responses to photoperiod change with phenophase and temperature during wheat development. *Field Crops Research* 46: 1–13.
- Slafer GA, Kantolic AG, Appendino ML, Tranquilli G, Miralles DJ, Savin R. 2015. Genetic and environmental effects on crop development determining adaptation and yield. In: Sadras VO, Calderini DF, eds. *Crop physiology: applications for genetic improvement and agronomy*. Amsterdam: Elsevier Inc, 285–319.
- Slafer GA, Casas AM, Igartua E. 2023. Sense in sensitivity: difference in the meaning of photoperiod insensitivity between wheat and barley. *Journal of Experimental Botany* 74: 3923–3932.
- Snape JW, Law CN, Parker BB, Worland AJ. 1985. Genetical analysis of chromosome 5A of wheat and its influence on important agronomic characters. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* 71: 518–526.
- Snape JW, Butterworth K, Whitechurch E, Worland AJ. 2001. Waiting for fine times: genetics of flowering time in wheat. *Euphytica* 119: 185–190.
- Song L, Liu J, Cao B, et al. 2023a. Reducing brassinosteroid signalling enhances grain yield in semi-dwarf wheat. *Nature* 617: 118–124.
- Song J, Li L, Liu B, et al. 2023b. Fine mapping of reduced height locus *RHT26* in common wheat. *Theoretical and Applied Genetics* 136: 62.
- Spielmeyer W, Ellis M, Robertson M, Ali S, Lenton JR, Chandler PM. 2004. Isolation of gibberellin metabolic pathway genes from barley and comparative mapping in barley, wheat and rice. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* 109: 847–855.

- Steinfart U, Trevaskis B, Fukai S, Bell KL, Dreccer MF. 2017. Vernalisation and photoperiod sensitivity in wheat: Impact on canopy development and yield components. *Field Crops Research* **201**: 108–121.
- Strayer C, Oyama T, Schultz TF, et al. 2000. Cloning of the Arabidopsis clock gene *TOC1*, an autoregulatory response regulator homolog. *Science* **289**: 768–771.
- Strejčková B, Milec Z, Holušová K, et al. 2021. In-depth sequence analysis of bread wheat *VRN1* genes. *International Journal of Molecular Sciences* **22**: 12284.
- Suárez-López P, Wheatley K, Robson F, Onouchi H, Valverde F, Coupland G. 2001. *CONSTANS* mediates between the circadian clock and the control of flowering in *Arabidopsis*. *Nature* **410**: 1116–1120.
- Sun F, Guo G, Du J, et al. 2014. Whole-genome discovery of miRNAs and their targets in wheat (*Triticum aestivum* L.). *BMC Plant Biology* **14**: 142.
- Takano M, Inagaki N, Xie X, et al. 2005. Distinct and cooperative functions of Phytochromes A, B, and C in the control of deetiolation and flowering in rice. *The Plant Cell* **17**: 3311–3325.
- Takata N, Saito S, Saito CT, Uemura M. 2010. Phylogenetic footprint of the plant clock system in angiosperms: evolutionary processes of *Pseudo-Response Regulators*. *BMC Evolutionary Biology* **10**: 126.
- Takeuchi T, Newton L, Burkhardt A, Mason S, Farre EM. 2014. Light and the circadian clock mediate time-specific changes in sensitivity to UV-B stress under light/dark cycles. *Journal of Experimental Botany* **65**: 6003–6012.
- Tan C, Yan L. 2016. Duplicated, deleted and translocated *VRN2* genes in hexaploid wheat. *Euphytica* **208**: 277–284.
- Tang S, Li L, Zhou QY, et al. 2019. Expression of wheat gibberellins 2-oxidase gene induced dwarf or semi-dwarf phenotype in rice. *Cereal Research Communications* **47**: 239–249.
- 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.
- Trevaskis B. 2010. The central role of the *VERNALIZATION1* gene in the vernalization response of cereals. *Functional Plant Biology* **37**: 479–487.
- Trevaskis B, Bagnall DJ, Ellis MH, Peacock WJ, Dennis ES. 2003. MADS box genes control vernalization-induced flowering in cereals. *Proceedings of the National Academy of Sciences of the United States of America* **100**: 13099–13104.
- Trevaskis B, Hemming MN, Peacock WJ, Dennis ES. 2006. *HvVRN2* responds to daylength, whereas *HvVRN1* is regulated by vernalization and developmental status. *Plant Physiology* **140**: 1397–1405.
- Trevaskis B, Tadege M, Hemming MN, Peacock WJ, Dennis ES, Sheldon C. 2007a. Short vegetative phase-like MADS-box genes inhibit floral meristem identity in barley. *Plant Physiology* **143**: 225–235.
- Trevaskis B, Hemming MN, Dennis ES, Peacock WJ. 2007b. The molecular basis of vernalization-induced flowering in cereals. *Trends in Plant Science* **12**: 352–357.
- Turner A, Beales J, Faure S, Dunford RP, Laurie DA. 2005. The pseudoresponse regulator *Ppd-H1* provides adaptation to photoperiod in barley. *Science* **310**: 1031–1034.
- Ueguchi-Tanaka M, Ashikari M, Nakajima M, et al. 2005. *GIBBERELLIN INSENSITIVE DWARF1* encodes a soluble receptor for gibberellin. *Nature* **437**: 693–698.
- Valárik M, Linkiewicz AM, Dubcovsky J. 2006. A microcolinearity study at the earliness per se gene *Eps-Aml* region reveals an ancient duplication that preceded the wheat–rice divergence. *Theoretical and Applied Genetics* **112**: 945–957.
- Valverde F, Mouradov A, Soppe W, Ravenscroft D, Samach A, Coupland G. 2004. Photoreceptor regulation of *CONSTANS* protein in photoperiodic flowering. *Science* **303**: 1003–1006.
- Wang ZY, Tobin EM. 1998. Constitutive expression of the *CIRCADIAN CLOCK ASSOCIATED1* (*CCA1*) gene disrupts circadian rhythms and suppresses its own expression. *Cell* **93**: 1207–1217.
- Wang J, Wen W, Hanif M, et al. 2016. *TaELF3-1DL*, a homolog of *ELF3*, is associated with heading date in bread wheat. *Molecular Breeding* **36**: 161.
- Whitechurch EM, Slafer GA. 2001. Responses to photoperiod before and after jointing in wheat substitution lines. *Euphytica* **118**: 47–51.
- Whitechurch EM, Slafer GA. 2002. Contrasting *Ppd* alleles in wheat: Effects on sensitivity to photoperiod in different phases. *Field Crops Research* **73**: 95–105.
- Wilhelm EP, Turner AS, Laurie DA. 2009. Photoperiod insensitive *Ppd-A1a* mutations in tetraploid wheat (*Triticum durum* Desf.). *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* **118**: 285–294.
- Wille Wille W, Pipper CB, Rosenqvist E, Andersen SB, Weiner J. 2017. Reducing shade avoidance responses in a cereal crop. *AoB Plants* **9**: plx039.
- Willige BC, Ghosh S, Nill C, et al. 2007. The DELLA domain of *GA INSENSITIVE* mediates the interaction with the *GA INSENSITIVE DWARF1A* gibberellin receptor of *Arabidopsis*. *The Plant Cell* **19**: 1209–1220.
- Winfield MO, Lu C, Wilson ID, Coghill JA, Edwards KJ. 2009. Cold- and light-induced changes in the transcriptome of wheat leading to phase transition from vegetative to reproductive growth. *BMC Plant Biology* **9**: 55.
- Wittern L, Steed G, Taylor LJ, et al. 2023. Wheat *EARLY FLOWERING 3* affects heading date without disrupting circadian oscillations. *Plant Physiology* **191**: 1383–1403.
- Woods DP, Li W, Sibout R, et al. 2023. *PHYTOCHROME C* regulation of photoperiodic flowering via *PHOTOPERIOD1* is mediated by *EARLY FLOWERING 3* in *Brachypodium distachyon*. *PLoS Genetics* **19**: e1010706.
- Worland AJ. 1996. The influence of flowering time genes on environmental adaptability in European wheats. *Euphytica* **89**: 49–57.
- Worland AJ, Law CN. 1986. Genetic analysis of chromosome 2D of wheat. I. The location of genes affecting height, day-length insensitivity, hybrid dwarfism and yellow-rust resistance. *Plant Breeding* **96**: 331–345.
- Worland AJ, Börner A, Korzun V, Li WM, Petrovic S, Sayers EJ. 1998. The influence of photoperiod genes on the adaptability of European winter wheats. *Euphytica* **100**: 385–394.
- Wu G, Park MY, Conway SR, Wang JW, Weigel D, Poethig RS. 2009. The sequential action of miR156 and miR172 regulates developmental timing in *Arabidopsis*. *Cell* **138**: 750–759.
- Wu L, Liu D, Wu J, et al. 2013. Regulation of *FLOWERING LOCUS T* by a microRNA in *Brachypodium distachyon*. *The Plant Cell* **25**: 4363–4377.
- Würschum T, Boeven PHG, Langer SM, Longin CFH, Leiser WL. 2015. Multiply to conquer: copy number variations at *Ppd-B1* and *Vrn-A1* facilitate global adaptation in wheat. *BMC Genetics* **16**: 96.
- Würschum T, Langer SM, Longin CFH, Tucker MR, Leiser WL. 2017. A modern Green Revolution gene for reduced height in wheat. *The Plant Journal: for Cell and Molecular Biology* **92**: 892–903.
- Würschum T, Langer SM, Longin CFH, Tucker MR, Leiser WL. 2018. A three-component system incorporating *Ppd-D1*, copy number variation at *Ppd-B1*, and numerous small-effect quantitative trait loci facilitates adaptation of heading time in winter wheat cultivars of worldwide origin. *Plant, Cell and Environment* **41**: 1407–1416.
- Xiao J, Xu S, Li C, et al. 2014. *O*-GlcNAc-mediated interaction between *VER2* and *TaGRP2* elicits *TaVRN1* mRNA accumulation during vernalization in winter wheat. *Nature Communications* **5**: 4572.
- Xie L, Zhang Y, Wang K, et al. 2021. *TaVrr2*, an SVP-like gene, cooperates with *TaVrn1* to regulate vernalization-induced flowering in wheat. *The New Phytologist* **231**: 834–848.
- Xing LJ, Li J, Xu YY, Xu Z, Chong K. 2009. Phosphorylation modification of wheat lectin *VER2* is associated with vernalization-induced *O*-GlcNAc signaling and intracellular motility. *PLoS One* **4**: e4854.
- Xu M, Hu T, Zhao J, et al. 2016. Developmental functions of miR156-regulated *SQUAMOSA PROMOTER BINDING PROTEIN-LIKE* (*SPL*) genes in *Arabidopsis thaliana*. *PLoS Genetics* **12**: e1006263.
- Yamaguchi S. 2006. Gibberellin biosynthesis in *Arabidopsis*. *Phytochemistry Reviews* **5**: 39–47.
- Yamaguchi S. 2008. Gibberellin metabolism and its regulation. *Annual Review of Plant Biology* **59**: 225–251.
- Yan J, Zhang S. 2017. Effects of dwarfing genes on water use efficiency of bread wheat. *Frontiers of Agricultural Science and Engineering* **4**: 126–134.
- Yan L, Loukoianov A, Tranquilli G, Helguera M, Fahima T, Dubcovsky J. 2003. Positional cloning of wheat vernalization gene *VRN1*. *Proceedings of the National Academy of Sciences of the United States of America* **100**: 6263–6268.
- Yan L, Helguera M, Kato K, Fukuyama S, Sherman J, Dubcovsky J. 2004a. Allelic variation at the *VRN-1* promoter region in polyploid wheat. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* **109**: 1677–1686.
- Yan L, Loukoianov A, Blechl A, et al. 2004b. The wheat *VRN2* gene is a flowering repressor down-regulated by vernalization. *Science* **303**: 1640–1644.

- Yan L, Fu D, Li C, *et al.* 2006. The wheat and barley vernalization gene *VRN3* is an orthologue of *FT*. *Proceedings of the National Academy of Sciences of the United States of America* **103**: 19581–19586.
- Yao Y, Guo G, Ni Z, *et al.* 2007. Cloning and characterization of microRNAs from wheat (*Triticum aestivum* L.). *Genome Biology* **8**: R96.
- Yong WD, Xu YY, Xu WZ, *et al.* 2003. Vernalization-induced flowering in wheat is mediated by a lectin-like gene *VER2*. *Planta* **217**: 261–270.
- Yoo SK, Chung KS, Kim J, *et al.* 2005. *CONSTANS* activates *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* through *FLOWERING LOCUS T* to promote flowering in *Arabidopsis*. *Plant Physiology* **139**: 770–778.
- Youssefian S, Kirby EJM, Gale MD. 1992. Pleiotropic effects of the GA-insensitive Rht dwarfing genes in wheat. 2. Effects on leaf, stem, ear and floret growth. *Field Crops Research* **28**: 191–210.
- Yu H, Xu YF, Tan EL, Kumar PP. 2002. *AGAMOUS-LIKE 24*, a dosage-dependent mediator of the flowering signals. *Proceedings of the National Academy of Sciences of the United States of America* **99**: 16336–16341.
- Yu JW, Rubio V, Lee NY, *et al.* 2008. *COP1* and *ELF3* control circadian function and photoperiodic flowering by regulating *GI* stability. *Molecular Cell* **32**: 617–630.
- Yu X, Liu H, Klejnot J, Lin C. 2010. The cryptochrome blue light receptors. *Arabidopsis Book* **8**: e0135.
- Yuan L, Liu X, Luo M, Yang S, Wu K. 2013. Involvement of histone modifications in plant abiotic stress responses. *Journal of Integrative Plant Biology* **55**: 892–901.
- Zahn T, Zhu Z, Ritoff N, *et al.* 2023. Novel exotic alleles of *EARLY FLOWERING 3* determine plant development in barley. *Journal of Experimental Botany* **74**: 3630–3650.
- Zhang Y, Ni Z, Yao Y, Nie X, Sun Q. 2007. Gibberellins and heterosis of plant height in wheat (*Triticum aestivum* L.). *BMC Genetics* **8**: 40–52.
- Zhang J, Wang Y, Wu S, Yang J, Liu H, Zhou Y. 2012. A single nucleotide polymorphism at the *vrn-D1* promoter region in common wheat is associated with vernalization response. *TAG. Theoretical and Applied Genetics. Theoretische und angewandte Genetik* **125**: 1697–1704.
- Zhang B, Wang X, Wang X, Ma L, Wang Z, Zhang X. 2018. Molecular characterization of a novel vernalization allele *vrn-B1d* and its effect on heading time in Chinese wheat (*Triticum aestivum* L.) landrace hongchunmai. *Molecular Breeding* **38**: 127.
- Zhang B, Guo Y, Fan Q, Li R, Chen D, Zhang X. 2023. Characterization and distribution of novel alleles of the vernalization gene *Vrn-A1* in Chinese wheat (*Triticum aestivum* L.) cultivars. *The Crop Journal* **11**: 852–862.
- Zhao XY, Liu MS, Li JR, Guan CM, Zhang XS. 2005. The wheat *TaG11*, involved in photoperiodic flowering, encodes an *Arabidopsis GI* ortholog. *Plant Molecular Biology* **58**: 53–64.
- Zhao YY, Wang X, Wei L, Wang JX, Yin J. 2016a. Characterization of *Ppd-D1* alleles on the developmental traits and rhythmic expression of photoperiod genes in common wheat. *Journal of Integrative Agriculture* **15**: 502–511.
- Zhao XY, Hong P, Wu JY, *et al.* 2016b. The *tae-miR408*-mediated control of *TaTOC1* gene transcription is required for the regulation of heading time in wheat. *Plant Physiology* **170**: 1578–1594.
- Zhao ZC, Duan S, Hao JM, *et al.* 2021. The dwarf gene *Rht15* improved lodging resistance but differentially affected agronomic and quality traits in durum wheat. *Field Crops Research* **263**: 108058.
- Zhao Z, Wen Q, Zhe L, *et al.* 2023. The interactions of *Rht15* and *Rht1* alleviate some of their negative effects on agronomic traits in durum wheat. *European Journal of Agronomy* **151**: 127000.
- Zhu Z, Esche F, Babbén S, *et al.* 2023. An exotic allele of barley *EARLY FLOWERING 3* contributes to developmental plasticity at elevated temperatures. *Journal of Experimental Botany* **74**: 2912–2931.
- Zikhali M, Leverington-Waite M, Fish L, *et al.* 2014. Validation of a 1DL earliness per se (*Eps*) flowering QTL in bread wheat (*Triticum aestivum*). *Molecular Breeding: New Strategies in Plant Improvement* **34**: 1023–1033.
- Zikhali M, Wingen LU, Griffiths S. 2016. Delimitation of the *Earliness per se D1* (*Eps-D1*) flowering gene to a subtelomeric chromosomal deletion in bread wheat (*Triticum aestivum*). *Journal of Experimental Botany* **67**: 287–299.
- Zikhali M, Wingen LU, Leverington-Waite M, Specel S, Griffiths S. 2017. The identification of new candidate genes *Triticum aestivum FLOWERING LOCUS T3-B1* (*TaFT3-B1*) and *TARGET OF EAT1* (*TaTOE1-B1*) controlling the short-day photoperiod response in bread wheat. *Plant, Cell and Environment* **40**: 2678–2690.

