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REVIEW

Molecular regulation of bud dormancy in perennial plants

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Abstract
Bud dormancy is an essential strategy for perennial plants to resist unsuitable growth environments, which is of great significance for the survival and reproduction of plants. Short days and low temperature are two of the most crucial environmental cues of bud dormancy; correspondingly, perennial plants are categorized into photoperiod-sensitive plants represented by poplars (*Populus* spp.), and temperature-sensitive plants represented by pear and peach. The existing evidence indicates significant differences in dormancy regulation between the two types of plants; nevertheless, similarities also be found and the key regulators of floral induction play essential roles in dormancy. Based on the latest findings, this review summarizes the genetic regulatory network mediating the control of bud dormancy of perennial plants from three stages, dormancy induction, endodormancy, and dormancy release. Hopefully, this work will contribute to exploring effective signal transduction pathways and critical target genes of environmental factors regulating bud dormancy, and provide a theoretical basis for further use of genetic engineering and environmental treatment to control the annual growth of perennials.

Keywords Bud dormancy · Low temperature · Molecular regulation · Perennial plants · Short day

Introduction

Unable to move, plants have evolved the capacity to respond to environmental signals and synchronize their growth with seasonal changes. In autumn, perennials growing in boreal and temperate regions cease growth and establish dormancy to overcome the frost of winter and protect buds from freezing injury. In contrast, prolonged low temperature in winter promotes dormancy release and enables plants to resume growth in spring (Singh et al. 2017).

Bud dormancy is defined as a state in which the cell divisions of shoot apical meristem (SAM) cease; however, the SAM does not respond or respond to different environmental cues at different stages of this state. It is usually considered that the bud dormancy of perennials includes three key stages: dormancy induction, endodormancy, and dormancy release; finally, the swelling of buds signifies the recovery of growth. During the stage of dormancy induction, although plants cease growth, they still maintain the ability to respond to external signals, and the growth cessation can be reversed by exposure to a suitable environment; usually, this stage is defined as the ecodormancy (Lang et al. 1987; Yamane et al. 2021). Subsequently, plants gradually establish endodormancy. In this state, the SAM is insensitive to external growth-promoting cues, and the growth arrest is controlled by endogenous signals; hence, growth cannot be reactivated even if the favorable conditions are provided (Lang et al. 1987; Horvath et al. 2003). As a result, dormancy must be terminated through dormancy release induced by dormancy release signals, which is usually prolonged cold exposure (Maurya and Bhalerao 2017). Despite plants responding

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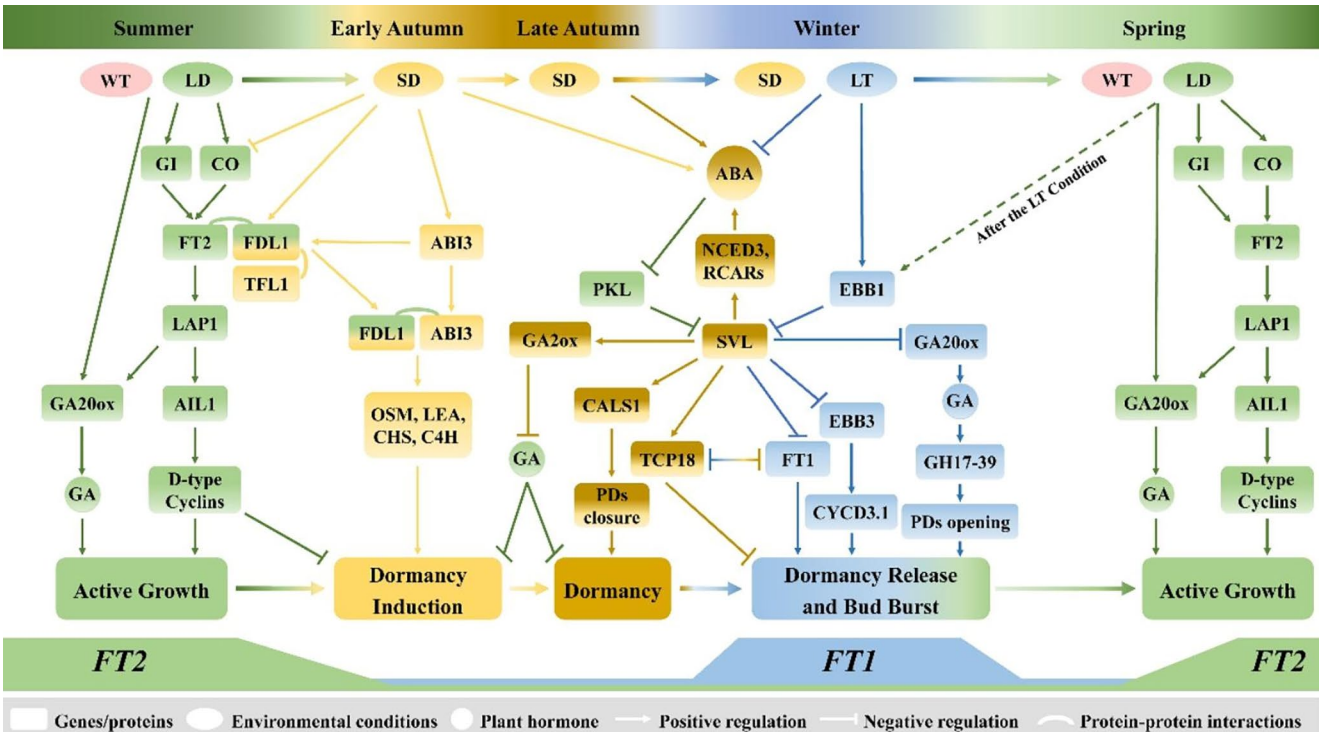

Fig. 1 The genetic network for seasonal growth-dormancy regulation based on studies in *Populus*

to external stimuli in both the release and induction stages of dormancy, the effects of external signals on SAM and the expression patterns of genes distinguish the two stages from each other (Howe et al. 2015; Singh et al. 2017). Once dormancy is released, the relatively warm temperature will restart plant growth: buds swell, leaf primordia emerge, and eventually, new leaves form and grow (Singh et al. 2017).

The dormancy of perennial plants, including the model tree poplar (*Populus* spp.), is mainly regulated by photoperiod and temperature (Heide 2011; Petterle et al. 2013; Ding and Nilsson 2016). The genetic regulation of dormancy has been intensively studied in poplar: the signal transduction pathways of photoperiod and temperature are intertwined to form a complex regulatory network, and finally converge the dormancy signals to key integration factors, such as *FLOWERING LOCUS T 1* (*FT1*), *FT2*, and *SHORT VEGETATIVE PHASE-LIKE* (*SVL*) in poplar, thereby regulating dormancy (Bohlenius et al. 2006; Tylewicz et al. 2018; Singh et al. 2018, 2019; Miskolczi et al. 2019; André et al. 2022; Gómez-Soto et al. 2022).

Although the regulatory pathways of dormancy have been discussed in stages by large amounts of literature, the genetic network of the entire dormancy process remains to be combed. In this review, we discuss photoperiod- and temperature-mediated regulation of the vital dormancy stages in perennials growing in temperate and boreal regions, and summarize the genetic network based on current findings (Fig. 1; Table 1). Subsequently, we find a massive overlap between the genetic networks of dormancy and floral induction. The critical signal integration factors of dormancy, such as the *CONSTANS* (*CO*) and *FT1* of poplar, also play central roles in integrating endogenous and exogenous signals in floral induction (Bouché et al. 2016). Additionally, photoperiod and temperature are the main exogenous signals for both dormancy and flowering. The findings lead us to hypothesize that dormancy and floral induction may share numerous regulatory factors and corresponding regulatory pathways; consequently, the systematic and comprehensive regulatory network of floral induction may enlighten the research on dormancy regulation.

In spring and summer, the growth-promotive signal, long days (LD), induces and maintains the expression of *FT2*, which acts as the central regulator of active growth; then, FT2 activates gibberellin (GA) biosynthesis and the *AP1/FUL-AIL* pathway, supporting the growth of trees. During late summer/early autumn, short days (SD) reduce the transcript abundance of *FT2* and then interrupt GA biosynthesis and *AP1/FUL-AIL* pathway, hence triggering dormancy induction (growth cessation). In late autumn, prolonged SD promotes dormancy establishment and maintains the stage by upregulating the expression of *SVP*. *SVL* is induced by the abscisic acid (ABA)-mediated SD signal, and acts as the hub for dormancy establishment and maintenance. On the one hand, *SVL* upregulates *CALS1* and downregulates *GH17-39* to isolate shoot apical meristems (SAM) by blocking Plasmodesmata (PDs). On the other hand, *SVL* induces

Table 1 Dormancy regulator genes and their functions

Species	Gene	Function	Mechanism	References
Populus spp.	*GI*	Maintaining the LD-mediated active growth.	GI proteins participate in the complex formation only in LD, and then induce *FT2* expression through a *CO*-independent pathway, thereby controlling growth cessation.	Ding et al. 2018.
	GI	Maintaining the LD-mediated active growth.	GI proteins participate in the complex formation only in LD, and then induce *FT2* expression through a *CO*-independent pathway, thereby controlling growth cessation.	Ding et al. 2018.
	CO	Maintaining the LD-mediated active growth.	CO proteins are accumulated only in LD and activate *FT2* transcription to suppress growth cessation.	Bohlenius et al. 2006.
	FT2	Maintaining the LD-mediated active growth.	*FT2* systemically induces active growth of shoot. As an early response, *FT2* is downregulated when the photoperiod shifts from LD to SD, and this downregulation is necessary for dormancy induction.	Bohlenius et al. 2006; Hsu et al. 2011; Miskolczi et al. 2019; André et al. 2022; Gómez-Soto et al. 2022.
	FDL1	Maintaining the LD-mediated active growth and participating in adaptive response and bud maturation.	Under LD condition, FDL1 interacts with FT2 to promote *LAP1* transcription; under SD condition, FDL1 interacts with ABI3 to mediate in the adaptive response and bud maturation.	Tylewicz et al. 2015.
	LAP1	Maintaining the LD-mediated active growth.	*LAP1* acts downstream of FT–FDL1 complex and controls SD-mediated dormancy induction through two pathways. *LAP1* directly induces *AIL1* to stimulate cell division in shoot apex; meanwhile, *LAP1* mediates in the transcriptional control of *GA20ox* to promote GA synthesis.	Azeez et al. 2014; Tylewicz et al. 2015; Miskolczi et al. 2019.
	GA20ox	Maintaining the LD-mediated active growth.	*GA20ox* encodes a key GA biosynthetic enzyme to regulate GA level. The bioactive GA acts as a member of the photoperiodic signal pathway to convey photoperiodic signal from leaves to the shoot apex and concomitantly acts locally in shoot apex, thus controlling seasonal growth.	Rinne et al. 2011; Miskolczi et al. 2019.
	AIL1	Maintaining the LD-mediated active growth.	As the target gene of LAP1, *AIL1* is inhibited by SD signal; meanwhile, AIL1 protein can active the downstream D-type cyclins. Therefore, AIL1 is the key regulator that connects the SD signal with the key cell cycle genes.	Karlberg et al. 2011; Azeez et al. 2014; Randall et al. 2015.
	TFL1	Promoting the SD-mediated dormancy induction.	TFL acts locally at the shoot apex and antagonizes with FT2 to accelerate the dormancy induction.	Rinne et al. 2011; Miskolczi et al. 2019.
	ABI3	Participating in adaptive response and bud maturation	ABI3, a component of ABA signaling, participates in the regulation of adaptive response and bud maturation via interaction with FDL1.	Ruttink et al. 2007; Tylewicz et al. 2015.
	NCED3	Establishing and maintaining the SD-mediated endodormancy.	*NCED3* encodes a key enzyme which is required for positive feedback regulation of ABA biosynthesis, and its expression decreases after exposure to LT.	Singh et al. 2018.
	RCARs	Establishing and maintaining the SD-mediated endodormancy.	As the key ABA receptors, RCARs involve in the ABA signaling pathway.	Singh et al. 2018.
	PKL	Suppressing the establishment and maintenance of endodormancy.	*PKL*, a negative regulator of *SVL*, is downregulated by ABA.	Singh et al. 2019.
	SVL	Establishing and maintaining the SD-mediated endodormancy.	*SVL* acts as the center of the signaling network for endodormancy establishment and maintenance. On the one hand, *SVL* is induced by ABA-mediated SD signal to promote expression of growth repressors *TCP18* and *CALS1*; simultaneously, *SVL* positively regulates ABA biosynthesis by inducing *NCED3* and *RCARs*, hence keeping its own expression at high level. On the other hand, *SVL* suppresses the expression of growth promoters, including *FT1*, *GA20ox*, *EBB3*, and *GH17-39*, resulting in the maintenance of endodormancy.	Singh et al. 2018; Singh et al. 2019; Azeez et al. 2021.
	CALS1	Establishing and maintaining the SD-mediated endodormancy.	*CALS1* mediates PDs closure via callose deposition to restrict access to growth-promotive signals.	Tylewicz et al. 2018; Singh et al. 2019.

Table 1 (continued)

Species	Gene	Function	Mechanism	References
	TCP18	Maintaining the SD-mediated endodormancy.	*TCP18* is a direct target of SVL and delays bud break by the potential manner of antagonizing FT1.	Singh et al. 2018.
	EBB1	Promoting LT-mediated dormancy release and bud burst.	*EBB1* provides a key link from the LT signal to *SVL* expression. EBB1 is induced by LT and directly suppresses *SVL* to promote dormancy release and bud burst.	Yordanov et al. 2014; Azeez et al. 2021.
	EBB3	Promoting LT-mediated dormancy release and bud burst.	*EBB3* is downstream of bud-break suppressors ABA and *SVL*, connects LT signal with the activation of cell division by directly inducing *CYCD3.1*.	Azeez et al. 2021.
	CYCD3.1	Promoting LT-mediated dormancy release and bud burst.	*CYCD3.1* promotes the G1/S progression of the cell cycle and hence correlates with reactivation of cell division in SAM.	Horvath et al. 2003; Azeez et al. 2021.
	GH17-39	Promoting LT-mediated dormancy release.	ABA-suppressed and GA-inducible *GH17-39* promotes callose hydrolysis to reopen signaling conduits in SAM.	Rinne et al. 2011; Tylewicz et al. 2018.
	FT1	Promoting LT-mediated dormancy release and bud burst.	Chilling induces *FT1* expression by inhibiting *SVL*, and this upregulation is absolutely required for dormancy release; additionally, although *FT1* has mobility, it functions locally within individual buds.	Hsu et al. 2011; Rinne et al. 2011; André et al. 2022.
Vitis vinifera	*VvFT*, *VvAP1*, *VvAIL2*	Maintain the LD-mediated active growth and promoting dormancy release.	These genes compose the *VvFT-VvAP1-VvAIL2* pathway, which transmit SD signal and hydrogen cyanamide signal to cell cycle genes in the shoot apex, and hence, regulating dormancy induction and dormancy release, respectively.	Vergara et al. 2016.
Pyrus pyrifolia	*PpDAM1*	Establishing and maintaining the LT- and SD-mediated endodormancy.	*PpDAM1* promotes the synthesis and signal transduction of ABA to control dormancy induction and release.	Saito et al. 2015; Tuan et al. 2017; Gao et al. 2021.
	PpEBB1	Promoting bud burst.	*PpEBB1* is dramatically induced by active histone modifications prior to the bud break and is associated with the increased promoter activities of D-type cyclin genes.	Tuan et al. 2016.
Actinidia chinensis	*AcSVP2*	Maintaining the endodormancy.	*AcSVP2* is predominantly expressed in dormant buds and then suppressed by epigenetic mechanisms, affecting the maintenance of bud endodormancy.	Wu et al. 2019
Amygdalus persica	*ApDAM6*	Establishing and maintaining the LT- and SD-mediated endodormancy.	*DAM6* expression increases and decreases concomitantly with dormancy establishment and release, respectively.	Leida et al. 2012.
Picea abies	*FT4*	Promoting the SD-mediated dormancy induction.	*FT4* is functionally more similar to *TFL* and mediates in SD-induced dormancy.	Gyllenstrand et al. 2007; Klintenas et al. 2012
Platanus acerifolia	*PaFT*	Promoting LT-mediated dormancy release and bud burst.	*PaFT* displays extremely high expression level during dormancy release and bud break, and may function through *FT-AP1/FUL-AIL* pathway.	Cai et al. 2019; Cai et al. 2021

LD, long days; SD, short days; LT, low temperature

growth inhibitor *TCP18* to maintain dormancy and suppresses growth promoters *FT1*, *EBB3*, and *GA2ox* to repress the release of dormancy. Prolonged cold exposure in winter induces *GH17-39*, *FT1*, *GA2ox*, and *EBB3* expression by declining the transcript abundance of *SVL*, leading to PDs reopening, CYCD3.1 activation, meristem activity, and dormancy release. Subsequently, bud break was promoted by warm temperature in the spring. WT, warm temperature; LD, long days; SD, short days; LT, low temperature.

Induction of bud dormancy

Numerous environmental factors affect dormancy induction, such as temperature and photoperiod, which have been identified as two of the most important. According to the main cues of dormancy induction, perennials growing in boreal and temperate regions are divided into two categories: (1) photoperiod-sensitive plants, represented by poplar and spruce (*Picea* spp.) (Ding and Nilsson 2016; Petterle et al. 2013), (2) temperature-sensitive plants, described by

some species of Rosaceae, such as apple (*Malus ×domestica*), pear (*Pyrus pyrifolia*) (Heide 2008, 2011).

Photoperiod Control of Dormancy induction

In temperate and boreal regions, the shortening day length announces the onset of winter. The photoperiod-sensitive perennials accurately sense and measure the change through leaves, and transduce SD signal to the shoot apex to trigger dormancy induction, which terminates apical elongation and induces the development of dormant buds (Ruttink et al. 2007; Petterle et al. 2013). The signal transduction depends on two pathways, mobile FT- and gibberellin (GA)-mediated pathways.

Photoperiod induces dormancy by *FT-AP1/FUL-AIL* pathway

In the model tree poplar, the molecular regulatory networks underlying the photoperiodic control of dormancy induction have been well elaborated in previous reviews (Maurya and Bhalerao 2017; Singh et al. 2017). Under the long days (LD) condition, CO and GIGANTEA (GI), two key regulators strictly controlled by circadian oscillators, induce the expression of *FT2* (an *FT* ortholog in poplars)(Bohlenius et al. 2006; Ding et al. 2018). FT2 protein can interact with FD-LIKE1 (FDL1) by antagonizing TERMINAL FLOWER 1 (TFL1), then the FT2-FDL1 complex actives the downstream *APETALA1* (*AP1*)/*FRUITFULL* (*FUL*)-like gene *LAP1* (Azeez et al. 2014; Tylewicz et al. 2015; Miskolczi et al. 2019). Subsequently, LAP1 directly induces the *AINTEGUMENTA-LIKE* gene *PtAIL1*, which promotes cell division in SAM by regulating D-type cyclin expression (Karlberg et al. 2011; Randall et al. 2015). Therefore, the *FT2-LAP1-PtAIL1* pathway with high expression levels maintains active apical growth.

The shortening day length in fall inhibits the expression of *FT2*, and the interruption of the *FT2-LAP1-PtAIL1* pathway results in dormancy induction. Additionally, FDL1 interacts with ABSCISIC ACID INSENSITIVE 3 (ABI3) under the SD condition, and form the FDL1-ABI3 complex to regulate the expression of genes responsible for bud maturation and cold acclimation (Tylewicz et al. 2015).

In non-model trees, such as grape (*Vitis vinifera*), SD suppresses the *VvFT-VvAP1-VvAIL2* pathway to cease growth (Vergara et al. 2016). In *Platanus acerifolia*, a similar *PaFTL-PaFUL2-PaAIL5* pathway also exists and responds to SD signal (our unpublished data); however, the *FD* homologs may not have the function of controlling bud maturation and cold acclimation (Cai et al. 2019, 2021). Interestingly, SD induces dormancy by upregulating *FT4* in the gymnosperm *Picea abies*, and one interpretation is that *FT4* is closer to *TFL* in function (Gyllenstrand et al. 2007; Klintenas et al. 2012). These observations indicate the conservation and divergence of the regulatory mechanisms underlying dormancy induction in different perennials.

Photoperiod induces dormancy by gibberellin

Phytohormones are vital regulators of seasonal growth, for example, gibberellin (GA) participates in the photoperiodic control of dormancy induction (Maurya and Bhalerao 2017). Under the influence of SD, concentrations of GA rapidly decline in leaves and shoot apices of poplars; in contrast, GA biosynthesis gene *GA20 oxidase* (*GA20ox*)-overexpressing plants (*GA20oxoe*) maintain high levels of GA and continue to grow (Eriksson and Moritz 2002). Furthermore, wild-type (WT) scions are grafted on rootstocks of *GA20oxoe*, leading to high GA concentrations and delayed growth cessation of WT scions under SD conditions. Thus, GA synthesized in the leaves can migrate to the shoot apex to regulate dormancy induction (Miskolczi et al. 2019).

GA plays a dual role, acting as both long-distance and local signaling components in dormancy induction of the shoot apex. The levels of bioactive GA are controlled either via *LAP1* or independently of *LAP1*. Under the SD condition, the expression levels of *GA20ox* in *FT* overexpressors and *LAP1* overexpressors are significantly higher than those of WT plants; additionally, there is no noticeable difference in the expressions of GA metabolism-related genes between transgenic and WT plants under LD conditions (Miskolczi et al. 2019). Consequently, both *FT* and its target *LAP1* are involved in regulate GA metabolism in the apex by SD. Since *LAP1* is primarily expressed in the shoot apex, the regulation of *LAP1* on GA metabolism is confined to the apex; thus, GA levels in leaves are controlled independently of *LAP1* (Miskolczi et al. 2019).

On the one hand, SD induces a reduction in GA level in leaves, thereby blocking GA mobility from leaves to the shoot apex. On the other hand, SD suppresses the GA synthesis by downregulating *FT* and its target *LAP1* in the shoot apex. These effects collectively strengthen the photoperiod-mediated induction of dormancy.

Temperature control of dormancy induction

In addition to the photoperiod, the temperature is another critical signal for seasonal changes. Low temperature, regardless of photoperiods, induces dormancy in apple, pear, and *Sorbus* spp. (Heide 2011; Heide and Prestrud 2005). The regulatory mechanism of temperature-induced dormancy remains poorly understood, but the signaling pathway may interact with other pathways, including the photoperiod pathway. Low temperature interferes with the

circadian rhythm of *LATE ELONGATED HYPOCOTYL* (*LHY*) and *TIMING OF CAB EXPRESSION 1* (*TOC1*) in *Castanea sativa* (Ramos et al. 2005), while the rhythm disorders of *LHY* and *TOC1* delay growth cessation and bud set in *Populus* (Ibanez et al. 2010). In some plants of Rosaceae, short days and low temperature co-regulate *DORMANCY ASSOCIATED MADS-box* (*DAM*) expression to inhibit growth and induce bud set (Yamane et al. 2021).

Establishment and maintenance of bud dormancy

The continued SD signal after growth cessation is essential to establish and maintain bud dormancy in poplar (Singh et al. 2017); for some species of Rosaceae, by contrast, low temperature is the most crucial signal (Yamane et al. 2021). Regardless of the type of plants, the establishment and maintenance of dormancy are achieved through the symplastic isolation of SAM, which is established by blocking Plasmodesmata (PDs) (Han et al. 2014; Tylewicz et al. 2018). PDs are microscopic channels connecting adjacent cells and are blocked or opened by deposition or degradation of callose. The Abscisic acid (ABA)-mediated SD signal can induce and maintain PDs closure via a complex regulation network, hence, interrupting the transport of regulatory molecules to establish and maintain bud dormancy (Roberto et al. 2007; Tylewicz et al. 2018).

SD induces the generation of dormancy-promotive signals

SD can upregulate ABA levels of the shoot apex in poplars (Ruttink et al. 2007; Karlberg et al. 2010). *ABI1* is a critical ABA-signaling gene. Compared with WT plants, the *abi1-1* mutant exhibits attenuated response to ABA and markedly low frequencies of PDs closure under SD conditions; furthermore, although *abi1-1* plants cease growth, they cannot enter the endodormancy phase (Tylewicz et al. 2018). In addition, the genes associated with PDs closure and controlled by SD, such as *CALLOSE SYNTHASE 1* (*CALS1*) and *GLUCAN HYDROLASE 17–39* (*GH17-39*) induced and suppressed by SD, respectively, show the altered expressions in the *abi1-1* mutant (Rinne et al. 2011; Tylewicz et al. 2018). Thus, ABA can regulate the callose metabolism-related genes to affect PD closure, thereby controlling the establishment and maintenance of dormancy rather than induction.

The expression pattern of the *Populus SVL* gene under SD conditions in *abi1-1* plants is also different from that in WT plants. The upregulation of *SVL*, the homologous gene of the floral repressor *SHORT VEGETATIVE PHASE* (*SVP*), is induced by SD in WT apices; in contrast, the upregulation of *SVL* is absent in the buds of *abi1-1* mutants (Singh et al. 2019). The phenotype of *SVL* RNA interference (RNAi) plants (*SVL*RNAi) is similar to that of *abi1-1* plants, namely, the endodormancy is not successfully established. Moreover, SVL protein directly promotes *CALS1* expression (Singh et al. 2019). Consequently, the upregulation of *SVL* mediated by the SD signal depends on ABA, and *SVL* participates in callose deposition to promote the establishment and maintenance of dormancy by regulating *CALS1*.

A positive feedback regulation is formed between *SVL* and ABA. Under SD conditions, *PICKLE* (*PKL*) gene, which encodes a chromatin remodeling factor, is upregulated in *abi1-1* mutants but downregulated in WT (Bouyer et al. 2011; Tylewicz et al. 2018). The low *SVL* expression level and endodormancy defects of *abi1-1* mutants are restored in *abi1-1*/*PKL* RNAi (*PKL*RNAi) plants with reduced *PKL* expression, suggesting that ABA promotes *SVL* expression by inhibiting *PKL* expression (Tylewicz et al. 2018; Singh et al. 2019). *NINE-CIS-EPOXYCAROTENOID DIOXYGENASE 3* (*NCED3*) encodes the pivotal ABA biosynthesis enzyme and *REGULATORY COMPONENT OF ABA RECEPTOR 1/2* (*RCAR1/2*) encodes the key ABA receptors involved in the ABA-activated signaling pathway (Singh et al. 2018). The expressions of *NCED3* and *RCAR1/2* are induced in *SVL*-overexpressing (*SVL*oe) apices but inhibited in *SVL*RNAi apices (Singh et al. 2018). Therefore, *SVL* upregulates ABA levels by positively regulating the genes related to ABA biosynthesis and signal transduction to.

In brief, SD-mediated increases in ABA concentrations can induce *SVL* upregulation, and in turn, *SVL* upregulates the ABA levels by promoting the expression of *NCED3* and *RCAR1/2*; hence, *SVL* and ABA form a positive feedback loop under SD conditions. Moreover, *SVL* directly regulates the transcription of *CALS1* to promote callose synthesis, ultimately leading to PDs closure and thus dormancy establishment.

SD inhibits the generation and transduction of growth-promotive signals

In addition to inducing dormancy-promotive signals, SD can also inhibit the generation of growth-promotive signals to maintain endodormancy. GA has been proven to be the systemic and local growth-promotive signals of seasonal shifts (Miskolczi et al. 2019). Under SD conditions, *SVL* represses the *GA20ox* expression and concomitantly induces the *GA2ox* expression to inhibit GA biosynthesis and promote GA catabolism, respectively; subsequently, GA levels drops, resulting in dormancy maintenance (Singh et al. 2019).

On the other hand, GH17-39 can unblock symplastic intercellular communication and resume regulator transport by hydrolyzing the callose deposited in PDs (Rinne et al. 2011), so that the SAM re-receives growth-promotive signals and reactivate the growth. Whereas SD signal prevents PDs from reopening by inhibiting *GH17-39* expression through an ABA-mediated pathway, thereby maintaining bud dormancy (Tylewicz et al. 2018).

The "dormancy" of Rosaceae floral buds

The floral bud consists of the floral meristem and organs in Rosaceae; their formation, differentiation, and development are started and completed during the autumn and winter; starch accumulation and hormone fluctuations are ongoing in the meanwhile (Rothkegel et al. 2020; Yu et al. 2020). In brief, the floral development and dormancy of Rosaceae floral buds are carried out simultaneously. Because of the continued metabolic activities, researchers have raised questions about whether the definition of dormancy applies to Rosaceae floral buds. However, the morphological observation on the floral buds of sweet cherry (*Prunus avium*) reveals that there is a specific "rest" stage in which floral development is temporally suspended (Fadón et al. 2018). Furthermore, the length of the "rest" stage seems to play important roles in the chilling requirement for bud dormancy release (Fadón et al. 2018). This particular phenomenon of Rosaceae floral buds has attracted the attention of researchers, but the underlying molecular mechanism is still unclear.

Dormancy release and bud burst

In winter, perennials such as poplars are exposed to prolonged cold, which induces dormancy release; the subsequent warm and LD signals promote bud burst (Singh et al. 2017; Yamane et al. 2021). Prolonged exposure to chilling causes the reopening of PDs to restore the response of SAM to growth-promotive signals and promote dormant release; however, it is worth noting that the reopening of PDs is the precondition but not the predisposing factor for dormancy release (Rinne et al. 2011; Cooke et al. 2012).

SD and low temperature antagonistically regulate*SVL*expression

SVL, the center of the signaling network for dormancy establishment and maintenance, regulates dormancy release and bud burst (Singh et al. 2018, 2019; Azeez et al. 2021). The expression of *SVL* is induced by SD but inhibited by chilling; in addition, the bud burst of *SVL*oe lines is distinctly delayed compared to WT poplars, whereas that of *SVL*RNAi lines is significantly earlier (Singh et al. 2018). These findings indicate that SD and low temperature antagonistically regulate *SVL* expression to control the transition from bud dormancy to dormancy release and subsequent bud burst (Singh et al. 2018).

Under exposure to cold, both ABA levels and *SVL* expression are reduced. ABA is a positive regulator of *SVL*, and the decline in ABA levels caused by a prolonged cold may be the basis for the downregulation of *SVL* expression. This downregulation involves *EARLY BUD-BREAK 1* (*EBB1*), a key promoter of bud burst. *EBB1* is downregulated under SD conditions and sharply upregulated in the cold; moreover, a warm environment after cold exposure can further increase *EBB1* expression (Azeez et al. 2021). *EBB1* overexpressors (*EBB1*oe) display the phenotype of early bud burst compared to WT plants, while *EBB1* RNAi plants (*EBB1*RNAi) delay bud burst. Consistent with the phenotypes, the expression of *SVL* is decreased in *EBB1*oe lines and increased in *EBB1*RNAi lines, respectively. Further experiments prove that EBB1 can directly regulate the transcription of *SVL* by binding to its promoter (Yordanov et al. 2014; Azeez et al. 2021). The results suggest that *EBB1* is induced by low temperature and promotes dormancy release and bud burst by directly inhibiting the expression of *SVL*. Moreover, the elevated levels of EBB1 proteins may break the feedback loop between *SVL* and ABA by suppressing *SVL*, leading to a further decline in ABA levels. Thus, *EBB1* not only directly affects the expression of *SVL* but may also indirectly reduce ABA levels, thereby regulating dormancy release and bud burst.

Low temperature induces dormancy release and bud burst by inhibiting*SVL*expression

A recent study on poplar mutants reveals that *EBB3* promotes dormancy release and bud break (Azeez et al. 2021). *EBB3* expresses in the shoot apex and acts downstream of *EBB1* and *SVL*; in addition, the annual expression pattern of *EBB3* is consistent with that of *EBB1* and opposite to that of *SVL* (Azeez et al. 2021). *EBB3* is subject to the epigenetic regulation mediated by low temperature; namely, cold triggers a significant decrease in the repressive mark H3 lysine 27 trimethylation (H3K27me3) at the *EBB3* locus, thereby promoting the transcription of *EBB3* (Azeez et al. 2021). Notably, EBB3 fills the gap between the low temperature signal and cell proliferation required for growth reactivation. EBB3 directly and positively regulates *CYCLIND3.1* (*CYCD3.1*), a key promoter of cell cycle progression, to activate cell proliferation in SAM (Azeez et al. 2021). In summary, *SVL* is suppressed by low temperature, leading to the induction of *EBB3* expression, while *EBB3* activates

CYCD3.1 expression and consequently promotes cell proliferation, dormancy release, and bud break.

In *Populus*, *TEOSINTE BRANCHED1*, *CYCLOIDEA*, *PCF 18*/*BRANCHED1* (*TCP18*/*BRC1*), and another *FT* homologous gene *FT1*, also act immediately downstream of *SVL* and participate in the regulation of dormancy release and bud burst. In the annual model plant *Arabidopsis thaliana*, TCP18/BRC1 interacts with FT to negatively regulate the activation of axillary buds, and its expression level rapidly declines after axillary bud outgrowth (Niwa et al. 2013). In poplar, low temperature inhibits the expression of *TCP18/BRC1* but induces *FT1* (Singh et al. 2018). Moreover, the bud burst of *TCP18/BRC1* overexpressors and *ft1* mutant plants are significantly delayed compared to WT plants (Singh et al. 2018; André et al. 2022), while *FT1*-overexpressing poplars continue growth under SD conditions (Hsu et al. 2011). These findings suggest that *FT1* and *TCP18/BRC1* may antagonize each other in regulating dormancy release and bud burst. In brief, mediated by *SVL*, low temperature induces *FT1* expression; meanwhile, chilling inhibits *TCP18/BRC1* to prevent its antagonism with *FT1*; eventually, the dormancy release and bud burst are caused.

Consequently, a question has been raised about the downstream regulators of *FT1*. Similar to caused *FT1*, another *FT* homologous gene of *P. acerifolia*, *PaFT*, is induced by low temperature to regulate dormancy release (Cai et al. 2019). The expressions of *PaFT*, *PaFUL2/3*, and *PaAIL5/6* were significantly upregulated at the dormancy release and bud break stages, suggesting that another *PaFT*-dominated *PaFT-PaFUL2/3-PaAIL5/6* pathway might be required for dormancy release and bud break (our unpublished data).

In addition, as the growth-promotive signals, GA promotes dormancy release and bud break. Without cold exposure, GA feeding induces abnormal growth of dormancy bud; besides, the expression of several genes associated with GA biosynthesis and reception is upregulated significantly during cold exposure (Rinne et al. 2011; Singh et al. 2018; André et al. 2022). *GA20ox*, for instance, displays the opposite expression trend compared to *SVL* under low temperature conditions (Singh et al. 2018). The phenomenon may be explained by the fact that chilling suppresses *SVL* expression and consequently relieves the inhibitory effect of SVL on *GA20ox*. Furthermore, the reduction of GA levels caused by *GA2ox* overexpression represses early bud burst in *SVL*RNAi plants (Singh et al. 2018). These results indicate that the growth-promotive GA is a critical target of *SVL* in low temperature-induced dormancy release and bud burst.

Epigenetic regulation induced by low temperature

The environmental cue inducing dormancy release is prolonged cold, also required for vernalization in floral induction. *FLOWERING LOCUS C* (*FLC*) acts as the hub of the vernalization pathway and is epigenetically inhibited by cold (Berry and Dean 2015). Thus, the regulation of dormancy release and bud burst may also involve epigenetics, and this inference has been confirmed by related studies on multiple species, especially Rosaceae plants. For example, the active histone mark H3 lysine 27 trimethylation (H3K27me3) in *PpEBB1* (an *EBB1* homologous gene in pear) is enriched before bud break, and then the expression level of *PpEBB1* reaches the peak to promote bud break (Tuan et al. 2016). In Rosaceae, *DAM* genes play a dual role in regulating dormancy induction and release (Yamane et al. 2021; Fang et al. 2022). *DAM* genes of pear, such as *PpDAM1*, promote ABA synthesis and signal transduction; notably, their expressions are inhibited by removing another active histone modification H3 lysine 4 trimethylation (H3K4me3) (Saito et al. 2015; Tuan et al. 2017; Gao et al. 2021). In peach (*Amygdalus persica*), *ApDAM6* shares a similar function and expression regulation with *PpDAM1* (Leida et al. 2012).

FLC, *DAM*, and *SVP* genes belong to the MIKC-type MADS-box transcription factor subfamily (Becker and Theißen 2003; Dong et al. 2022). In *Actinidia chinensis*, *AcSVP2* negatively regulates dormancy release; the reduction in active histone modifications results in decreased expression of *AcSVP2*, thereby inducing dormancy release (Wu et al. 2019). Nevertheless, the inhibitory effect of low temperature on poplar *SVL* seems unrelated to epigenetics (Singh et al. 2018). In contrast, the expression of its downstream EBB3 involves chilling controlled epigenetic regulation (Azeez et al. 2021).

Conclusions and perspectives

During the past decade, photoperiod- and temperature-mediated regulation of bud dormancy has been deeply investigated, the substantial progress has been made in understanding the three critical stages in the model plant poplar. In *Populus* trees, *FT-AP1*/*FUL-AIL* pathway is responsible for maintaining LD-mediated active growth, while the *SVL* gene (*SVP* ortholog) acts as the hub for SD-mediated endodormancy. Nevertheless, the regulation mechanism underlying bud dormancy of other species is still poorly understood; further studies are needed to decipher the specific "dormancy" stage of Rosaceae floral bud and the associated molecular mechanisms. Studies of multiple species have shown that although dormancy regulation has exhibited conservation to a certain degree, there

is still species-specificity; therefore, it is uncertain whether the findings on poplar dormancy are applicable to other perennials.

It is noteworthy that the bud dormancy and the floral induction share critical regulatory factors that receive and transmit photoperiod and, or temperature signals. This phenomenon has been observed in several plants, indicating that critical molecular components have always played a key role in regulating various biological processes. Therefore, the commonality between bud dormancy and floral induction will also be a research hotspot in the future. Additionally, phytohormones, such as GA and ABA, have been confirmed to play essential roles in dormancy regulation; however, their molecular pathways are still unclear. The hormone pathway of flowering-time gene networks has been preliminarily elucidated, and results and experience can be used as a reference for further studies on hormone-mediated bud dormancy.

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Declarations

Conflict of Interest All authors state that there is no conflict of interest.

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