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REVIEW ARTICLE

Flowering and flowering genes: from model plants to orchids

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Abstract
Floral transition in model plants including *Arabidopsis* and rice has been studied extensively through molecular genetic approaches. Many genetic factors in different flowering pathways, which depend mainly on photoperiod, vernalization, autonomous and ambient temperature are regulated coordinately to control floral induction. However, for the ornamental plants orchids, the molecular mechanisms underlying the floral transition are still unclear. Recently, genes with potential flowering-related functions have been identified in different orchid species and their functional roles have also been characterized/examined using homologous or heterologous systems. In this review, we summarize the molecular networks of flowering genes and their regulation as revealed in model plants such as *Arabidopsis* and rice, and also describe the recent discoveries/studies on flowering genes in several commercially representative orchid species providing a perspective on orchid flowering research. In addition, our recent results through transgenic approaches with ectopic expression of *Hd3a*, a rice florigen gene for the induction of precocious flowering in *Phalaenopsis* orchids are also discussed.

Keywords Floral induction · Flowering genes · Orchids · Ornamental plants · Transgenic plants

1 Introduction

Transition from vegetative growth to the reproductive stage of flowering plants is usually influenced by environmental factors such as photoperiod and ambient temperature. The endogenous molecular signaling network in response to the different cues has been studied extensively in the model plant, *Arabidopsis* (Andres and Coupland 2012). In parallel, understanding of molecular mechanisms underlying flowering regulations in agricultural crops including rice has also been widened (Cho et al. 2017). Interestingly, some genetic factors are conserved, such as *FLOWERING LOCUS T* (*FT*) which encodes a strong candidate for florigen that triggers floral induction. Other species-specific or genus-specific factors are also required for flowering across various plant species.

The Orchidaceae is one of the largest families in angiosperms. Flowers of plants belonging to the family display a high degree of speciation, with wide variations in floral features including color, shape, size and fragrance to attract pollinators (Cozzolino and Widmer 2005). Floral induction is an important step leading to proper flower development in orchids; however, the molecular mechanism still remains to be elucidated. In general, juvenility, ambient temperature and photoperiod are known to be crucial for determining flowering time in orchids. In recent studies, many flowering-related genes in orchids have been identified and characterized. In this review, a summary of the major research findings involved in the regulation of orchid floral induction is presented together with representative flowering genes of model plants. In addition, results gained from our recent transgenic approaches with *Phalaenopsis* orchids are also included.

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2 Key players in the flowering of *Arabidopsis*

2.1 Florigen

The model plant *Arabidopsis* is an excellent material for studying flowering control because of its short life cycle and the various tools available for genetic studies. Floral transition in *Arabidopsis* is controlled by photoperiod, ambient temperature and vernalization. Among the regulatory networks, the *FT* gene is the strongest candidate to be 'florigen', the hypothesized master regulator of flowering in plants. The *FT* gene encodes a small globular protein belonging to the phosphatidylethanolamine-binding protein (PEBP) family (Mathieu et al. 2007). In *Arabidopsis*, *FT* is expressed in leaves and the FT protein is transported to the shoot apical meristem (SAM) where *FT* activates the transcription of *SOC1* (*SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1*) and floral meristem identity gene *AP1* in cooperation with a basic leucine zipper (bZIP) transcription factor *FD* (Abe et al. 2005; Lee and Imaizumi 2018; Yoo et al. 2005). Of note, it was recently shown that *FT* activity is likely to be regulated differentially for flowering in different plant species indicating that it may have evolved and integrated into different regulatory circuits in distinct plant species for flowering under their own favorite conditions (Jang et al. 2015).

2.2 Photoperiodic flowering regulator *CONSTANS*

Transcription factor *CONSTANS* (*CO*) regulates floral transition under the control of photoperiod. *CO* activates the expression of *FT* and *SOC1* and causes early flowering under long-day (LD) conditions (Samach et al. 2000; Suarez-Lopez et al. 2001; Tiwari et al. 2010). Subsequently, *LEAFY* (*LFY*), a meristem identity gene is activated by *SOC1* (Lee and Lee 2010). *CO* itself is activated and repressed by *FLOWERING bHLH (FBH)* and CYCLING DOF (DNA-binding one zinc finger) FACTOR (*CDF*), respectively (Fornara et al. 2009; Ito et al. 2012). *GIGANTEA (GI*) and *FLAVIN-BINDING KELCH REPEAT F-BOX 1* (*FKF1*) also activate *CO* directly (Sawa et al. 2007). Under inductive LDs, the peak expression of GI and FKF1 protein coincides resulting in the accumulation of the GI-FKF1 complex regulating the degradation of CDF. Recently, CINCINNATA (CIN) clade of class II TEOSINTE BRANCHED 1/CYCLOIDEA/PROLIFERATING CELL NUCLEAR ANTIGEN FACTOR (TCP) protein has been shown to activate the expression of *CO* in the association of *FBH* and *GI* (Kubota et al. 2017; Liu et al. 2017).

In addition to transcriptional control, post-transcriptional regulation of *CO* is also crucial for flowering time determination. The ubiquitin E3 ligase *CONSTITUTIVE PHOTOMORPHOGENIC 1(COP1*) cooperates with *SUPPRESSOR OF PHYA-105 1* (*SPA1*) to promote CO degradation (Zuo et al. 2011). COP1 also promotes GI degradation with the aid of EARLY FLOWERING 3 (ELF 3) (Yu et al. 2008). On the other hand, CO protein is stabilized by photoreceptors such as phytochromes and cryptochromes (Valverde et al. 2004). The *FKF1* has also been shown to stabilize the CO protein by inhibiting COP1-dependent CO degradation to regulate the photoperiodic flowering (Lee et al. 2018; Song et al. 2012).

Most regulators of *CO* are controlled by the system of the circadian clock in plants. In the morning, the expression of *CDF* is high while the expression of *GI* and *FKF1* is low. However, a reversed situation is observed in the afternoon (Niwa et al. 2007). Expression of *CO*, therefore, is increased in the late afternoon and maintained until dusk. Light-dependent stabilization of the rhythmically expressed *CO* is needed for *FT* activation, resulting in floral induction. Indeed, phytochrome and cryptochrome photoreceptors contribute to stabilize CO by retarding the activity of SUPPRESSOR OF PHYA-105 1 (COP1-SPA1) ubiquitin ligase complex, which promotes degradation of CO (Ponnu 2020; Zuo et al. 2011). More recently, it was found that *FT* expression peaks in the morning during spring in open-field LD condition through the combined action of phytochrome A and ELF3 (Song et al. 2018). Under the condition, CO protein is likely more stable in the morning that may contribute to the induction of *FT*. Thus, *CO* is a key component occupying in the photoperiodic flowering pathway.

Gibberellins (GAs) are a class of diterpenoid plant hormones that regulate a wide range of developmental processes including floral induction in *Arabidopsis*. However, it is known that GAs do not have a conserved floral promoting function in plants (Blazquez et al. 1998; Mutasa-Gottgens and Hedden 2009). Moreover, although GA promotes floral transition from vegetative to reproductive development, it inhibits the transition to flower formation in *Arabidopsis* reflecting the complexity of GA signaling involved in plant development (Yamaguchi et al. 2014). The GA singling is believed to play a role in converging photoperiodic pathway to regulate the floral induction by degrading the DELLA proteins (Nohales and Kay 2019).

2.3 Floral repressor *FLOWERING LOCUS C*

2.3.1 Vernalization pathway

In *Arabidopsis*, *FT* and two other flowering integrators *FD* and *SOC1* are negatively regulated by *FLOWERING LOCUS C* (*FLC*), a MADS-box gene (Helliwell et al. 2006). Constant expression of *FLC* prevents the winter-annual *Arabidopsis* from flowering before winter season, and repression is released by prolonged cold temperature

termed vernalization. During and after vernalization, the chromatin changes occur at *FLC* with a reduced level of histone acetylation and increased levels of the repressive methylation in H2K9 and H3K27 (Coupland 2019; Sung and Amasino 2004). Three plant homeodomain (PHD) finger-containing proteins including *VERNALIZATION INSENSETIVE* (*VIN3*), *VERNALIZATION 5* (*VRN5*) and *VERNALIZATION 5/VIN3 LIKE 1* (*VEL1*) in association with four polycomb repressive complex 2 (PRC2)-like subunits *SWINGER* (*SWN*), *VERNALIZATION 2* (*VRN2*), *FERTILIZATION INDEPENDENT ENDOSPERM* (*FIE*) and *MULTICOPY SUPPRESSOR OF IRA 1* (*MSI1*) are involved in the vernalization-dependent pathway (Questa et al. 2016). The SWN subunit is a homolog of *Drosophila* E(z) protein which contains histone 3 lysine 27 (H3K27) methyltransferase activity. The PHD-PRC2 protein complex represses the activity of *FLC* by the H3K27 trimethylation (H3K27me3) of *FLC* chromatin (Finnegan and Dennis 2007). This repression is further maintained by the *LIKE HETEROCHROMATIN 1* (*LHP1*) which recognizes the H3K27me3 mark (Yuan et al. 2016). The epigenetic modification of *FLC* by vernalization is stably maintained until embryogenesis so that *FLC* is re-activated in the next generation. Recently, an intronic noncoding RNA of *FLC* termed *COLD ASSISTED INTRONIC NONCODING RNA* (*COLDAIR*) has been shown to be required for the vernalization-mediated repression of *FLC* through its interaction with the PRC2-like complex (Heo and Sung 2011). Interestingly, a PRC2-like complex containing CURLY LEAF (CLF), EMBRYONIC FLOWER 2 (EMF2) and FIE has been shown to repress the *FT* activity by mediating the deposition of H3K27me2 during vegetative growth (Liu et al. 2018). Although the CLF-PRC2 complex is associated with *FLC* repression, *CLF* mutations induce early flowering of *Arabidopsis* suggesting that the CLF-PRC2 complex has a stronger repressive effect on *FT* than on *FLC* chromosomes.

2.3.2 Autonomous pathway

To activate floral transition, *FLC* can also be repressed by the autonomous pathway which means photoperiod-independent. Components of the autonomous pathway include RNA binding proteins FCA, FPA and FLOWERING LOCUS K (FLK), polyadenylation factor FY, homeodomain protein Luminidependens (LD), chromatin remodeling proteins FLOWERING LOCUS D (FLD) and FVE. The autonomous pathway suppresses *FLC* through histone modifications and RNA-processing regulation (Cheng et al. 2017). An antisense RNA of *FLC* termed *COLD INDUCED LONG ANTISENSE INTEGENEIC RNA* (*COOLAIR*) is generated with two major alternative splicing forms depending on the usage of proximal or distal polyadenylation site (Liu et al. 2010; Wu et al. 2020). *COOLAIR* with proximal polyadenylation is important for the repressive state of *FLC* (Liu et al. 2010), and it is promoted by the autonomous pathway (Liu et al. 2007). With the action of *FCA*, *FY* and a splicing factor *pre-mRNA processing 8* (*PRP8*), generation of proximal polyadenylated site of *COOLAIR* is increased, which leads to the *FLD*-dependent demethylation of H3K4me2 of *FLC* chromatin (Marquardt et al. 2014). H3K4me2 and H3K4me3 are the marks of transcriptional activation. The demethylation of H3K4me2 and generation of *COOLAIR* with proximal polyadenylation site splicing are regulated by a positive feedback. Moreover, *COOLAIR* was shown to mediate the function of PRC2-regulated vernalization (Tian et al. 2019).

2.3.3 *FRIGIDA* activates *FLOWERING LOCUS C*

The expression of *FLC* is promoted by the *FRIGIDA* (*FRI*) which encodes a coiled-coil protein through the modification of *FLC* chromatin (Li et al. 2018). *FRI* is defective in the rapid cycling *Arabidopsis* accessions such as Columbia and Landsberg *erecta*; so that vernalization is not necessary to facilitate flowering and they can complete the life cycle within one season. To activate *FLC*, FRI interacts with several *FLC*-specific regulators including FRI-LIKE 1 (FRL1), DNA binding protein SUPPRESSOR OF FRIGIDA 4 (SUF4), and transcriptional activators FLC EXPRESSOR (FLX) and FRIGIDA ESSENTIAL 1 (FES1) to form a FRI-complex (FRI-C) (Choi et al. 2011). The FRI-C recruits the SWR complex (SWR-C) and general transcriptional factors to *FLC*; sequentially, the *FLC* chromatin is marked with H3K4me3, H3K36me2, histone 3 acetylation (H3ac) and H4ac. All of these histone modifications are associated with transcriptional activation. SWR-C is a homolog of yeast ATP-dependent chromatin modifier SWR1 complex. The components of SWR-C include *PHOTOPERIOD-INDEPENT EARLY FLOWERING 1*(*PIE1*), *SUPPRESSOR OF FRIGIDA 3 (SUF3*), *SWC6* and *ACTIN-RELATED PROTEIN 4* (*ARP4*) (Choi et al. 2007). SWR-C also catalyzes the replacement of H2A with H2AZ, which leads to the activation of *FLC* (Deal et al. 2007). The protein level of FRI is negatively regulated by proteosome-mediated degradation during vernalization, and the degradation is accompanied by the up-regulation of *FLC COLDAIR* (Hu et al. 2014). A cullin-RING-type E3 ubiquitin ligase CUL3A and light response BTB proteins (LRBs) are responsible for promoting FRI degradation by interacting with FRI (Hu et al. 2014).

2.3.4 Polymerase II associated factor 1 complex activates the *FLOWERING LOCUS C*

The components and functions of the RNA Polymerase II associated factor 1 complex (Paf1 complex, Paf1c) are conserved from yeasts through to humans and plants (He et al. 2004; Tomson and Arndt 2013). Paf1c is known to be

required for the recruitment of histone modification factors and also for small RNA-mediated gene silencing process (Kowalik et al. 2015; Tomson and Arndt 2013). Indeed, Paf1c suppresses floral transition by activating *FLC* transcription through H3K4me3 enrichment in *FLC* chromatin in *Arabidopsis* (He et al. 2004). Components of Paf1c include *EARLY FLOWERING 7* (*ELF7*), *EARLY FLOWERING 8*/*VERNALIZATION-INDPENDENT 6* (*VIP6*), *VIP3*, *VIP4* and *VIP5* (Oh et al. 2004). ELF7 and VIP6 of Paf1c are also involved in the activation of *FLOWERING LOCUS M*/*MAF1* (*FLM*) and *MAF2* to *MAF5* but not *SUPPRESSOR OF VEGETATIVE PHASE* (*SVP*) and *AGAMOUS LIKE* (*AGL*) (He et al. 2004). Most of these are MADS-box genes and they act as flowering suppressors like *FLC*. Unlike *FLC*, however, *FLM* is involved in the regulation of photoperiodic flowering, as well (Scortecci et al. 2003).

2.3.5 *FLOWERING LOCUS T* homologs

Several homologs of *FT* have been identified in *Arabidopsis* including *TERMINAL FLOWER 1* (*TFL1*), *TWIN SISTER OF FT* (*TSF*), *MOTHER OF FT AND TFL1* (*MFT*), *BROTHER OF FT AND TFL1* (*BFT*) and *ARABIDOPSIS THALIANA CENTRORADIALIS HOMOLOGUS* (*ATC*) (Wickland and Hanzawa 2015). Among these genes, *FT* and *TFL1* are the major determinants of flowering time under LD conditions (Kim et al. 2013). Interestingly, *TFL1*, *BFT* and *ATC* function more like floral repressors but not activators. Furthermore, *FT* and *TFL1* also play antagonistic roles in the determination of inflorescence meristem identity affecting plant architecture (Lee et al. 2019); Their antagonistic functions are likely achieved through the binding competition with FD protein (Moraes et al. 2019). The *SVP* has been shown to repress *FT* and *TSF* by activating the *FT* repressors *TEMPRANILLO 2* (*TEM 2*) under the low-ambient temperature (16 °C) for *Arabidopsis* (Jang et al. 2009; Marin-Gonzalez et al. 2015). An alternatively spliced form of *FLM*, *FLM-β* may contribute to the control of flowering by low-ambient temperature together with SVP (Lee et al. 2013). Pre-mRNA of *FLM* is spliced into *FLM-β* or *FLM-δ* depending on the usage of different exons. The ratio of *FLM-β* to *FLM-δ* is increased at low-ambient temperature but decreased at high-ambient temperature. Although both FLM-β and FLM-δ interact with SVP, SVP suppresses the expression of floral activators only with FLM-β. Meanwhile, the bHLH transcription factor *PHYTOCHROME INTERACTING FACTOR 4* (*PIF4*) has been recently shown to regulate the floral transition under high-ambient temperature (Kumar et al. 2012). This indicates that sophisticated mechanisms are available in *Arabidopsis* for floral induction responding to the changes in ambient temperature. Of note, transcriptional activity of PIF4 has been shown to be suppressed by DELLAs, while GAs promoted the PIF4 activity by removing the DELLAs (de Lucas et al. 2008) suggesting convergence between the GA pathway and ambient temperature pathway in the control of flowering.

2.3.6 High expression of osmotically responsive gene 1 can activate *FLOWERING LOCUS C*

A RING-finger E3 ubiquitin ligase *high expression of osmotically responsive gene 1* (*HOS1*) has been demonstrated to play a role in activating *FLC* under short-term and intermittent cold stress (4 °C for several hours to few days) (Jung et al. 2013). Compared to vernalization, short-term cold stress causes the induction but not suppression of *FLC* resulting in delayed flowering (Lee and Park 2015). HOS1 interacts with *FLC* chromatin and FVE, a component of the autonomous flowering pathway. This interaction may result in the dissociation of histone deacetylase 6 (HDAC6) from *FLC* chromatin, which leads to the de-repression of *FLC*. The *HOS1* also has been shown to regulate CO degradation under short-term cold stress leading to delayed flowering (Lazaro et al. 2012). All of these findings suggest that the *HOS1* is crucial for the fine-tuning of flowering under short-term temperature fluctuations. The regulatory network of flowering control in *Arabidopsis*, showing the photoperiod, vernalization, autonomous and ambient temperature dependent pathways, is presented in Fig. 1.

3 Key players in the flowering of rice

Extensive research made it possible to isolate several regulatory genes involved in flowering, which are organized into a molecular network responsive to environmental cues. Several flowering genes are evolutionarily conserved between rice and *Arabidopsis* while other pathways with species/genus-specific genes have evolved independently and confer specific characteristics to flowering responses (Cho et al. 2017).

At least, two orthologs of *FT* are available in rice: *Heading date 3a* (*Hd3a*) and *RICE FLOWERING LOCUS T* (*RFT*). *Hd3a* and *RFT* are responsible for the induction of flowering under short-day (SD) and LD conditions, respectively (Sun et al. 2014). *Hd3a* is regulated by *Hd1*, a homolog of *CO* in rice. *Hd1* activates *Hd3a* under SD conditions, but not under LD conditions. Under LD conditions, *Hd3a* is down-regulated by *Hd1*. The repressive function of *Hd1* on *Hd3a* may be due to the action of red-light receptor PhyB, which leads to an increase in Hd1 protein since *Hd3a* is inhibited by overexpressed *Hd1* (Ishikawa et al. 2011).

OsGI activates *Hd1* and overexpression of *OsGI* causes the repression of *Hd3a* through the induced expression of *Hd1* resulting in late flowering irrespective of photoperiod, which is distinguishable from the result in *Arabidopsis*.

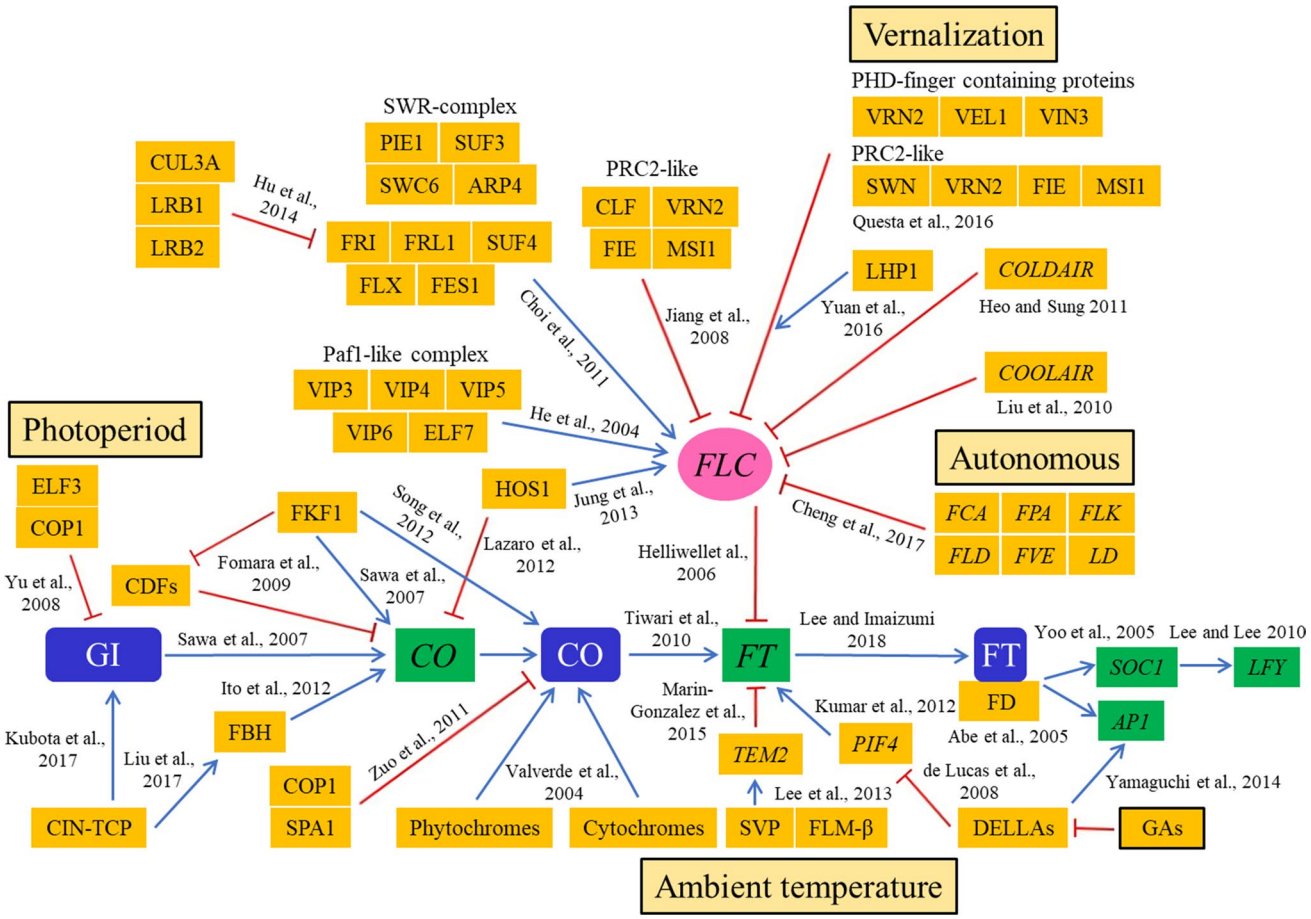

Fig. 1 Representative regulatory networks with focusing on photoperiod,vernalization, autonomous, GAs and ambient temperature dependent pathways inthe flowering control of *Arabidopsis*. Blue-colored lines ending with an *arrow indicate activation*, whereasred-colored ones ending with a perpendicular line *indicate repression*. Thereferences for each pathway are presented in the figure

Recently, a NF-YB transcription factor DAYS TO HEADING 8 (DTH8) has been shown to interact with Hd1, and the formation of the DTH8-Hd1 complex is essential for the transcriptional repression of *Hd3a* through the increased H3K27me3 of *Hd3a* chromatin in LD (Du et al. 2017).

Both *Hd3a* and *RFT* are activated by a rice-specific gene *Early heading date 1* (*Ehd1*) which encodes a B-type response regulator (Doi et al. 2004). The flowering time of rice is delayed under both LD and SD conditions if the *Ehd1* is mutated. Expression level of *Ehd1* is crucial for its function and, several flowering regulators are involved in the *Ehd1*-dependent pathway. *Ghd7* that encodes a CONSTANS, CO-Like, and TOC (CCT) domain protein, represses *Ehd1* under LDs. Previous studies showed that *Ghd7* interacts with *Hd1* to suppress the expression of *Ehd1* (Nemoto et al. 2016). The *Ghd7* itself is suppressed by a PHD finger protein Early heading date 3 (Ehd3) (Sun et al. 2014). Recently, it was demonstrated that OsGI and phytochromes antagonistically regulate Ghd7 protein stability (Zheng et al. 2019b); OsGI interacts with Ghd7 promoting the degradation of Ghd7, while phytochromes compete with OsGI in binding to Ghd7. Thus, under the non-inductive LDs, phytohormones prevent the degradation of Ghd7, resulting in delayed heading date of rice. Another putative repressor of *Ehd1* is *Oryza sativa LEC2 and FUSCA3 Like 1* (*OsLFL1*) which encodes a B3 transcription factor (Peng et al. 2008). *Ehd1* is activated by *OsMADS51* and *RICE INDETERMINATE 1* (*RID1*) (Park et al. 2008). *OsMADS51* acts downstream of *OsGI* to activate *Ehd1* (Kim et al. 2007) and also the DTH8-Hd1 module seems to act as a flowering activator under SDs (Du et al. 2017).

Besides *Hd1* and *Ehd1*, there are some other regulators of *Hd3a* and *RFT1*. For example, *DTH2* activates *Hd3a* and *RFT1* under LDs whereas *OsCO3* activates *Hd3* and *RFT1* under SDs (Kim et al. 2008; Wu et al. 2013). The *Hd3a* is also positively and negatively regulated by *Oryza sativae DNA-binding with one finger 12* (*OsDof12*) and *Oryza sativae pseudo-response regulator 37* (*OsPRR37*), respectively (Koo et al. 2013; Li et al. 2009).

Histone modifications at chromatins of key flowering genes such as *FLC* and *FT* are crucial for flowering regulation in *Arabidopsis*. Although no *FLC* orthologs are available and no vernalization is required for flowering in rice, histone modifications of rice *FT* orthologs such as *Hd3a*, *RFT* and other floral regulators play important roles in flowering time control (Komiya et al. 2008). Several genes encoding histone methyltransferase have been reported to regulate the heading time of rice by acting on specific flowering regulators. The SET domain protein SDG724 (SET domain group protein 724) is involved in the H3K36me2/3 of *RFT1* and *OsMADS50* (Sun et al. 2012a). Another SET domain protein SDG725 is involved in the H3K36me2/3 of *RFT1*, *OsMADS50*, *Ehd3* and *Hd3a* (Sui et al. 2013) and the SDG708 regulates the H3K36m3 level of *Hd3a*, *RFT1* and *Ehd1* (Liu et al. 2016). All these three SET domain group proteins promote the flowering of rice. *LC2/OsVIL3* (*VIL*, *VERNALIZATION INSENSITIVE 3-LIKE*), a putative component of rice PRC2 complex as a PHD finger protein suppresses the *Oryza sativae Late Flowering* (*OsLF*) expression via H3K27me3 (Sun et al. 2014). Since *OsLF* suppresses *Hd1*, *LC2/OsVIL3* also promotes flowering of rice under SDs. Another PHD finger protein *OsVIL2* and a C2H2 zing-finger protein *OsEMF2b*, which are possible members of rice PRC2 complex, suppress *OsLFL1* via H3K27me3 (Yang et al. 2013). Suppression of *OsLFL1* is required for the expression of *Ehd1*, *RFT1* and *Hd3a*. In short, similar to that of *Arabidopsis*, a putative rice PRC2 complex is also involved in the floral induction of rice in spite of different target genes for chromatin modifications.

4 Flowering control in orchids

4.1 Effect of phytohormones in the floral transition of orchids

Orchids have a worldwide distribution, and they occur in a wide variety of habitats. Thus, difference in the regulation of flowering among distinct species in the family may exist that evolved based on their natural habitats. The effect of ambient temperature or photoperiod on the flowering of different orchids has been reported (Hsiao et al. 2011). Moreover, effects of phytohormones on flowering in different orchids have been also investigated (Blanchard and Runkle 2008; Goh and Yang 1978). However, the molecular genetic mechanisms underlying the flowering of orchids are still largely unknown.

Most orchids take several years to reach the reproductive stage from the juvenile stage. *Phalaenopsis* orchids, for example, usually begin to bloom after the production of three to five leaves. In the flowering season, the floral spike (inflorescence) protrudes from the axillary buds of the fourth node below the apical leaf while other axillary buds are maintained in dormancy. The mechanism of differential commitment of distinct axillary buds for flowering remains elusive. At the early stage of flowering, the axillary buds are enlarged and then protrude from the base of a leaf, which takes about 3 to 4 weeks. Subsequently, the bud is elongated to be a floral spike.

Benzylaminopurine (BA), a synthetic cytokinin, triggers the floral induction of monopodial (e.g., *Phalaenopsis*) and sympodial (e.g., *Dendrobium*) orchids whereas auxin suppresses the effect of BA (Goh and Yang 1978). The effect of BA on floral induction can be enhanced when combined with gibberellic acid (GA_3) despite GA_3 alone not having an effect on floral induction (Hew and Clifford 1993). However, GA_3 treatment delayed flowering of *Cymbidium niveomarginatum* prepared for *in vitro* early flowering (Kostenyuk et al. 1999).

Phalaenopsis and *Doritaenopsis* orchids applied with BA produce visible inflorescences 3 to 9 days earlier than those of the control. Notably, the effect of BA on flowering promotion was inhibited when plants were incubated at 29 °C indicating that low ambient temperature is still required for floral induction of *Phalaenopsis* and *Doritaenopsis* even in the presence of BA (Blanchard and Runkle 2008).

The existence of abscisic acid (ABA) in different tissues of *Phalaenopsis* has been investigated. It was revealed that dormant axillary buds have relatively higher level of free ABA whereas free or bound forms of ABA were not detected in floral shoots (Wang et al. 2002). Moreover, exogenously applied ABA to the stem of *Phalaenopsis* repressed the formation of floral spikes even under inductive low ambient temperature conditions indicating that ABA may play a role in inhibiting floral induction in the orchid. In summary, the two phytohormones, cytokinin and ABA are involved in flowering regulation in orchids; however, ambient temperature seems to be a more critical factor for floral transition in *Phalaenopsis*.

4.2 Floral transition of orchids is regulated by ambient temperature and photoperiod

The floral induction of *Phalaenopsis* is promoted by low ambient temperature (usually lower than 26 °C). However, it can be reversed if the ambient temperature is increased (Blanchard and Runkle 2006). Floral induction based on the changes of ambient temperature has also been studied in *Dendrobium*, *Miltoniopsis* and *Zygopetalum* (Campos and Kerbauy 2004; Lopez and Runkle 2006; Lopez et al. 2003).

In model plants such as *Arabidopsis* and rice, photoperiod is one of the most critical factors controlling flowering time. However, in general, photoperiod has limited effects on flowering in orchids. Floral initiation regulated by photoperiod has been observed in just a few orchid species.

In *Doritis pulcherrima* (now *Phalaenopsis pulcherrima*), floral spikes were initiated more efficiently in the 9 h light /15 h dark cycle than that of 12 h light /12 h dark under the 30 °C light and 20 °C dark conditions (Wang et al. 2003). In *Miltoniopsis* orchids, SD incubation at 23 °C before moving to cool temperature (11–14 °C) facilitated flowering (Lopez and Runkle 2006). However, during the cool temperature treatment, different photoperiods had no significant effect on flowering implying that ambient temperature may play a prominent role in flowering of *Miltoniopsis*. On the other hand, the floral induction in *Psymorchis pusilla* was enhanced in prolonged day-length indicating that *P. pusilla* is a quantitative LD plant (Vaz et al. 2004). The effect of photoperiod on flowering appears to vary among different orchid species possessing great diversity in adaptation. Moreover, most orchids are native to tropical areas where photoperiod does not change dramatically during the year. Therefore, it is reasonable to expect that photoperiod may not influence the flowering of orchids significantly.

Many orchids are epiphytic plants. Shortages of nutrients and water are frequent in their living environment. Although the orchid uses the crassulacean acid metabolism (CAM) as the way for carbon fixation to adapt to the arid conditions (Silvera et al. 2009), flowering still requires a lot of energy. Thus, the right timing for flowering with the best physiological status is important for successful sexual propagation. In addition, in the wild most orchids have particular pollinators; the flowering time should be consistent with the appearance of their pollinators. Therefore, sensing ambient temperature can be a good strategy for successful pollination if their pollinators appear only in a particular season.

4.3 The flowering-related genes of *Phalaenopsis*

Based on the results obtained from analyses of sequence similarities, spatiotemporal expression patterns and functional studies using heterologous expression systems, many orchid flowering candidate genes have been reported. Although the flowering regulatory networks and their various components revealed in *Arabidopsis* and other model plants may provide clues to estimate functional roles of the players in orchid flowering, functional studies on target genes using target orchid species are absolutely required to verify their functions in orchid flowering.

Recently, an *FT* gene in *Phalaenopsis aphrodite* (*PaFT1*) has been characterized (Jang et al. 2015). Flowering of *P. aphrodite* is induced by prolonged low ambient temperature (< 26 °C) whereas photoperiod has no significant effect. Expression of *PaFT1* is induced by low ambient temperature and the flowering time of *P. aphrodite* was delayed by transient knockdown of *PaFT1*. Ectopic expression of *PaFT1* by a phloem-specific *Arabidopsis SUC2* promoter suppressed the delayed flowering caused by overexpression of *SVP* as well as an active *FRI* allele in *Arabidopsis* (Truernit and Sauer 1995); moreover, overexpression of *PaFT1* also triggered precocious heading in rice. Physical interaction between PaFT1 and PaFD also has been demonstrated. All these indicate that *PaFT1* is an important floral integrator in *Phalaenopsis* with a similar mode of *FT* action in *Arabidopsis* (Fig. 2).

PhapLFY, a *LFY* gene from *P. aphrodite* also has been isolated and characterized (Jang 2015). Induced expression of *PhapLFY* driven by *Arabidopsis LFY* promoter rescued the abnormal floral phenotype of *Arabidopsis lfy-32* mutant and induced early heading in rice by overexpression. In

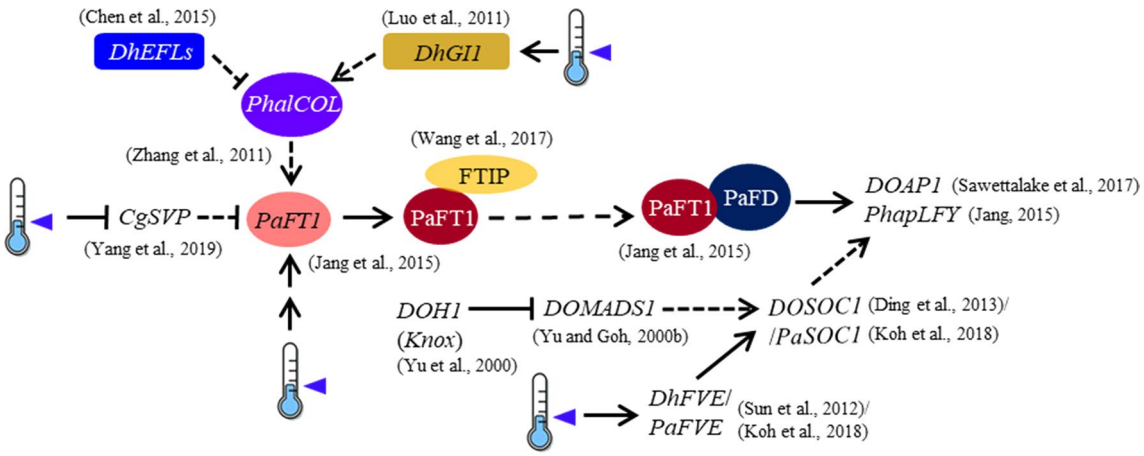

Fig. 2 Representative floweringregulatory genes in several orchid species. Solid lines indicate documentedpathways and dotted lines represent possible/hypothetical connections. Lines ending with an *arrow indicate activation*, and lines endingwith a perpendicular line *indicate repression. Each thermometer with a bluearrow head presents low ambient temperature.* The references for eachpathway are presented in the figure

addition, a *CO*-like gene, *PhalCOL* was isolated from *P. hybrida* (Zhang et al. 2011). Expression of *PhalCOL* was observed in all organs throughout development. Of note, high level accumulation of its transcripts was detected in the stem during the transition from vegetative to reproductive growth. Moreover, overexpression of *PhalCOL* in tobacco induced an early-flowering phenotype suggesting that *PhalCOL* plays a crucial role in promoting flowering of *Phalaenopsis*. Recently, the homolog of *FVE* in *P. aphrodite* also has been characterized (Koh et al. 2018). Expression of *PaFVE* was induced by low ambient temperature and ectopic expression of *PaFVE* in *Arabidopsis* generated an early-flowering phenotype. Furthermore, a recent report demonstrated that transcripts of *Spike activator 1*(*SPK1*) encoding a bHLH transcription factor are highly accumulated at the meristematic tissues including axillary bud responding to the floral inductive low ambient temperature in *P. aphrodite* (Lin et al. 2019) indicating it may play a role in early axillary bud development and/or spike initiation of the orchid. To explore candidate genes which may function in flowering control of *Phalaenopsis*, expression profiles of axillary buds from plants treated with or without cold temperature were analyzed (Huang et al. 2016). The results showed that, in addition to the *FT*, *LFY*, *AP1* and *SOC1*, genes involved in the GA biosynthetic pathway were also up-regulated by low ambient temperature. In another study, gene expression in spikes of *Phalaenopsis* orchids under warm day/cool night and daily warm temperature was analyzed (Li et al. 2014). Many candidate flowering-related genes including *FT*, *AP1* and *AP2* were found to be up-regulated in the induced spikes. In addition, highly accumulated transcripts of genes encoding KNOX1 protein, R2R3-like MYB transcription factor, adenosine kinase 2, S-adenosylmethionine synthetase, dihydroflavonol 4-reductase and naringenin 3-dioxygenase were observed although their functions in orchid flowering remain elusive.

The mechanism of flowering control also has been investigated in *Dortiaenopsis*, an intergeneric hybrid between the orchid genera *Doritis* and *Phalaenopsis* (*Dor*×*Phal*). *DhFVE*, a *Dortiaenopsis* ortholog of *FVE* has been identified and characterized (Sun et al. 2012b). Flowering of *Dortiaenopsis* is accelerated by low ambient temperature and the accumulation of *DhFVE* transcript reaches higher levels in the vegetative organs such as roots, stems, and leaves during the transition from vegetative to reproductive growth. Moreover, low ambient temperature-induced accumulation of *DhGI1* transcripts was also reported, which may be involved in the floral initiation of *Doritaenopsis* (Luo et al. 2011).

In addition, *ELF4* family genes including *DhELF2*, *DhELF3* and *DhELF4* have been identified in *Dortiaenopsis* (Chen et al. 2015). *Arabidopsis ELF4* is regarded as a key player acting in the integration of photoperiod, circadian regulation and flowering. Ectopic expression of *DhELF2*, *3*, or *4* delayed the flowering time in *Arabidopsis*.

4.4 The flowering-related genes of *Dendrobium*

Flowering of *Dendrobium nobile* is promoted but not required by low ambient temperature (Campos and Kerbauy 2004). The orthologs of *FT* and *MFT* identified in *Dendrobium* were designated as *DnFT* and *DnMFT* (Li et al. 2012). Expression of *DnFT* was increased in leaves but decreased in axillary buds under low temperature (Li et al. 2012; Wen et al. 2017). In contrast, expression of *DnMFT* was not affected by low temperature. Overexpression of *DnFT* resulted in early-flowering in *Arabidopsis*. So far, experiments using homologous expression system have only been applied in *Dendrobium* Chao Praya Smile, where *DOFT* overexpression causes early flowering (Wang et al. 2017). Interestingly, *DOFT* is also involved in the formation of pseudobulb. FT-INTERACTING PROTEIN1 (FTIP1) is known to be specifically required for FT transport from companion cells to sieve elements through plasmodesmata in *Arabidopsis* (Liu et al. 2012). Recently, DOFTIP1 has been identified as an interacting protein of DOFT indicating DOFT and DOFTIP1 are conserved for the flowering of *Dendrobium* (Wang et al. 2017; Fig. 2). In addition, an ortholog of *SOC1* in *Dendrobium* has also been identified designated as *DOSOC1* (Ding et al. 2013). Expression of *DOSOC1* was particularly induced in the shoot apex at the floral transition stage and the overexpression of *DOSOC1* in both *Arabidopsis* and *Dendrobium* caused early flowering. The role of *DOAP1*, the *AP1* gene in *Dendrobium*, has been reported to be similar to its ortholog of *Arabidopsis* (Sawettalake et al. 2017). Through the investigation of gene expression between vegetative and transitional shoot apical meristems in *Dendrobium* grex Madame Thong-In, several genes that code for transcription factors including a MADS-domain protein of the AP1/AGL2 family, a class I KNOX protein and a homolog of the *Drosophila* SEVEN-UP were found to be differentially expressed during floral transition (Yu and Goh 2000). Especially, the *KNOX* gene encoding a knotted1-like homeobox protein was designated as *Dendrobium* orchid homeobox 1 (*DOH1*) and known to play an important role in the maintenance of proper function of SAM. In tissue culture condition, the expression of *DOH1* is gradually up-regulated in the apical meristem during orchid vegetative development, whereas it is down-regulated with the progress of reproductive growth (Yu et al. 2000). Overexpression of *DOH1* antisense transcript promoted flowering in *Dendrobium*. *DOMADS1*, another MADS-box gene belonging to *AP1*/*AGL19* family in *Dendrobium* was preferentially expressed in transitional SAM during floral transition. Interestingly, expression of *DOMADS1* was induced in the transgenic plant containing p*35S*::antisense

DOH1 implying that *DOH1* is a potential repressor acting upstream of *DOMADS1* in the flowering control of *Dendrobium* orchids.

4.5 The flowering-related genes of *Oncidium*

High ambient temperature (30 °C) and LD conditions promote the flowering of *Oncidium*. Of note, the response of flowering to the changes of ambient temperature in *Oncidium* is contrary to that in *Phalaenopsis*. The *FT* and *TFL1* identified in *Oncidium* were designated as *OnFT* and *OnTFL1*, respectively (Hou and Yang 2009). Expression of *OnFT* is detected in axillary buds, leaves, pseudobulbs and flowers, and is also induced by light. On the contrary, the expression of *OnTFL1* is detected only in axillary buds and pseodobulbs and is not affected by light. Ectopic expression of *OnFT* caused early-flowering in *Arabidopsis* and could also rescue late-flowering of *Arabidopsis ft-1* mutants. *Arabidopsis TFL1* acts as a floral repressor and ectopic expression of *OnTFL1* in *Arabidopsis* also resulted in late-flowering (Kim et al. 2013). The expressions of *TFL1*-like genes in some neotropical orchids have also been examined (Ospina-Zapata et al. 2020). The results showed the expression patterns of *TFL1*-like genes are diverse in selected orchid species and these genes have been suggested to play a role in repressing floral transition.

An *Oncidium* homolog of *Arabidopsis AGL6*, *OMADS1* has been identified. The transcript of *OMADS1* was detected in the apical meristem and floral organs (Hsu et al. 2003). Transgenic *Arabidopsis* plants overexpressing *OMADS1* exhibited early flowering with up-regulated expression of *FT*, *SOC1*, *LFY* and *AP1*. Moreover, Thiruvengadam et al. demonstrated that ectopic expression of *OMADS1* in *Oncidium* also caused early flowering (Thiruvengadam et al. 2012).

Recently, ascorbic acid (AsA) content has been exhibited to play a key role in the floral transition of *Oncidium* in response to thermal stress (30 °C more than 14 days) (Chin et al. 2014). Under thermal stress, the level of reactive oxygen species (ROS, e.g., H_2O_2) was highly elevated and the AsA redox ratio (reduced form of AsA to dehydroascorbate/DHA) was reduced with a significant increase of *cytosolic ascorbate peroxidase 1* (*cytAPX1*). The oxidation of AsA to DHA by ascorbate peroxidase is the pivotal reaction to remove hydrogen peroxide. This report suggested that the AsA/dehydroascorbate redox ratio may function as an endogenous signal to induce the flowering in *Oncidium* responding to high ambient temperature. Furthermore, reduced glutathione (GSH) redox ratio was also shown to be linked to the decline in the AsA redox ratio by reduced expression of GSH metabolism-related genes such as *glutathione reductase* (*GR1*), *γ-glutamylcysteine synthase* (*GSH1*) and *glutathione synthase* (*GSH2*) to affect flowering in *Oncidium* orchid (Chin et al. 2016). Collectively, the results indicate that a stress-response mechanism is likely to be leveraged in *Oncidium* orchids to regulate floral transition.

4.6 The flowering-related genes of other orchids

Recently, many flowering-related genes have been identified in *Cymbidium* and *Erycina* through genome-wide studies; i.e., homologs of *FT*, *FCA*, *FYF*, *DCL3A*, and *VIN3* in *Cymbidium* (Li et al. 2013) and many MADS-box genes in *Erycina* (Lin et al. 2016). Prolonged low ambient temperature is also required for the flowering of *Cymbidium*. The expression of *SVP*-like genes in *C. goeringii* (*CgSVP*) is negatively regulated in response to low ambient temperature suggesting *CgSVP* suppresses floral induction during vegetative growth (Yang et al. 2019; Fig. 2). The functional roles of these genes in the flowering control in *Cymbidium* or *Erycina* need to be further investigated.

5 Conclusion and perspectives

Precise control of flowering time in response to environmental cues is essential for successful reproduction in plants. Thus, regulatory networks involved in sensing and responding to changes in photoperiod and/or temperature for floral induction are necessarily required and have evolved for distinct plant species based on their habitats. In orchids, it seems that the flowering network has evolved in a sophisticated manner to sense subtle differences in ambient temperature although many orchids are photoperiod-insensitive in floral induction. Also, all orchids are perennial plants, different from the annual model plant, *Arabidopsis*. Recent studies demonstrating potential mechanisms underlying flowering control in a perennial plant *Arabis alpina* have been reported (Bergonzi et al. 2013; Wang et al. 2011). In *A. alpine*, *AaTFL1* acts as a flowering repressor to ensure *A. alpina* is matured enough to go into the reproductive stage. It is worth investigating whether the *TFL1* in orchids also plays a role in determining the dormancy of axillary buds. Recently, the *TFL1*-like pathway has been implicated in the repressive function of floral induction in *Dendrobium* through gene expression studies (Zheng et al. 2019a). In addition, histone modifications are crucial for regulations of flowering-related genes in model plants. Thus, chromatin modifications are also likely to be a mechanism controlling the expression of flowering genes in orchids. Furthermore, a mechanism linked to stress-responses may be a strategy adapted by orchids to regulate floral transition. Recently, a protocol for the transformation of *Phalaenopsis* orchids was reported (Hsing et al. 2016), which is a breakthrough for functional studies on *Phalaenopsis* flowering genes.

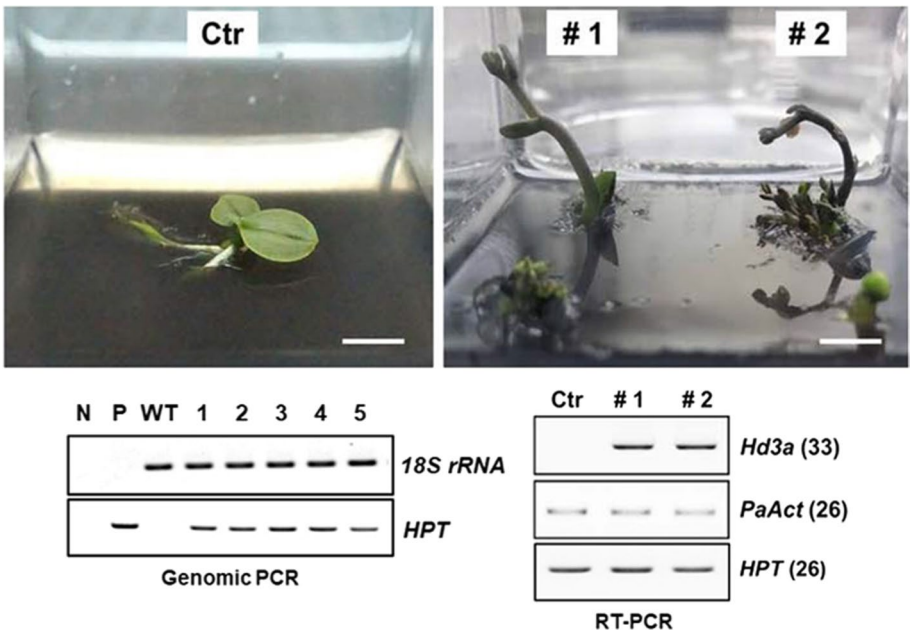

Fig. 3 Transgenic *Phalaenopsis* orchids (*P. aphrodite*) overexpressing *Hd3a* encoding a rice florigen. Transgenic orchids were verified by genomic PCR using five independent plantlets showing precocious flowering (No. 1 to 5). N and P indicate a negative (no template) and a positive (plasmid DNA) control for the genomic PCR. WT means a non-transgenic wild type *Phalaenopsis* orchid. Two independent transgenic orchids (#1 and #2) with high expression of the transgene produced inflorescence without generating leaves. Ctr is a transgenic *Phalaenopsis* orchid containing an empty vector as a control. Hygromycin was used to select transgenic plants as reported previously (Hsing et al. 2016). The following primers were used for genomic and RT-PCR, respectively: (*18S rRNA*-geF) 5'-TTAGGCCACGGAAGTTTGAGG, (*18S rRNA*-geR) 5'-ACACTTCACCGGACCATTCAA; (*Hpt*-geF, for *Hygromycin phosphotransferase*) 5'-ATCGCCTCGCTCCAGTCAATG, (*Hpt*-geR) 5'- AGCTGCGCCGATGGTTTCTACAA; (*Hd3a*-RTF) 5′-cggaagtggcagggacagg, (*Hd3a*-RTR) 5′-GTAGACCCTCCTGCCGCC; (*Act*-RTF, for *PaAct*) 5′-CTAGCGGAAACGCGACAGA, (*Act*-RTR) 5′-CCAAGGGAAGCCAAAATGC; (*Hpt*-RTF) 5'-GATTCCGGAAGTGCTTGACATTG, (*Hpt*-RTR) 5'-GCATCAGCTCATCGAGAGCCTG. Numbers in the parentheses are cycle numbers for PCR. Bar = 1 cm

Using the protocol, we generated transgenic *Phalaenopsis* orchids overexpressing a rice florigen gene, *Hd3a* (Fig. 3). The transgenic orchids produced spikes without vegetative growth during the transformation, which is similar to the phenotype of transgenic rice overexpressing *Hd3a* (Jang et al. 2017). Also, the result demonstrated that increased expression level of florigen is able to overcome the requirement of low ambient temperature for the flowering of *P. aphrodite*. We believe that this result is an example showing huge potential for functional studies of *Phalaenopsis* genes using the homologous system.

In short, it seems that there are various mechanisms for flowering control among different orchid species. Therefore, understanding of the flowering control in distinct orchids may provide a insights into strategic changes in the developmental evolution of the flowering of plants.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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