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Review

Co-ordination of Flower Development Through Epigenetic Regulation in Two Model Species: Rice and Arabidopsis

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Angiosperms produce flowers for reproduction. Flower development is a multistep developmental process, beginning with the initiation of the floral meristems, followed by floral meristem identity specification and maintenance, organ primordia initiation, floral organ identity specification, floral stem cell termination and finally floral organ maturation. During flower development, each of a large number of genes is expressed in a spatiotemporally regulated manner. Underlying these molecular and phenotypic events are various genetic and epigenetic pathways, consisting of diverse transcription factors, chromatin-remodeling factors and signaling molecules. Over the past 30 years, genetic, biochemical and genomic assays have revealed the underlying genetic frameworks that control flower development. Here, we will review the transcriptional regulation of flower development in two model species: *Arabidopsis thaliana* and rice (*Oryza sativa*). We focus on epigenetic regulation that functions to co-ordinate transcription pathways in flower development.

Keywords: Arabidopsis • Epigenetic regulation • Floral homeotic protein • Flower development • Organ identity control • Rice.

Abbreviations: AG, AGAMOUS; AHL1–29, AT-HOOK MOTIF NUCLEAR-LOCALIZED PROTEIN 1–29; AP, APETALA; BRM, BRAHMA; CHR, CHROMATIN REMODELING; CLF, CURLY LEAF; *clk*, *clark kent*; DAD1, DELAYED ANTHER DEHISCENCE 1; DH1, DEGENERATED HULL1; DL, DROOPING LEAF; EMF2, EMBRYONIC FLOWER2; ESC, extra sex comb; E(Z), enhancer of zeste; F3H, FLAVANONE 3 HYDROXYLASE; FIE, FERTILIZATION INDEPENDENT ENDOSPERM; FIS2, FERTILIZATION INDEPENDENT SEED2; FLC, FLOWERING LOCUS C; FM, floral meristem; FT, FLOWERING LOCUS T; GIK, GIANT KILLER; GR, glucocorticoid receptor; HAT, histone acetyltransferase; HDA, histone deacetylase; HDAC1, histone deacetylase 1; H3K4, methylation of histone H3 lysine 4; H3K9, methylation of histone H3 lysine 9; H3K27, methylation of histone H3 lysine 27; H3K36, methylation of histone H3 lysine 36; HMT, histone methyltransferase; I-domain, Intervening domain; IM, inflorescence meristem; JA, jasmonic acid; JmjC, Jumonji-C; K-domain, Keratin-like domain; KNU, KNUCKLES; KYP, KRYPTONITE; LEC2, LEAFY COTYLEDON2; LFY, LEAFY; MEA, MEDEA; MRG1/2, MORF-RELATED GENE 1 and 2; MSI1–5, MULTICOPY SUPPRESSOR OF IRA1–5; PcG, Polycomb group; PI, PISTILLATA; PKL, PICKLE; PRC, Polycomb Repressive Complex; PRE, Polycomb-Responsive Element-like element; REF6, RELATIVE OF EARLY FLOWERING 6; RLE, Repressive LEC2 Element; SDG728, SET DOMAIN GROUP 728; SEP, SEPALLATA; SEU, SEUSS; SPL/NZZ, SPOROCYTLESS/NOZZLE; STK, SEEDSTICK; SYD, SPLAYED; sup, superman; SU(Z)12, suppressor of zeste 12; SWN, SWINGER; TEK, TRANSPOSABLE ELEMENT SILENCING VIA AT-HOOK; TPL, TOPLESS; trxG, trithorax group; TSS, transcription start site; ULT1, ULTRAPETALA1; VRN2, VERNALIZATION2; WUS, WUSCHEL.

Conservation and Diversification of Floral Homeotic Proteins in Arabidopsis and Rice

The model plant Arabidopsis has a typical eudicotyledon Brassicaceae flower with four types of floral organs arranged in concentric whorls: a first whorl of four sepals, a second whorl of four petals, a third whorl of six stamens and a fourth whorl of two fused carpels (**Fig. 1A**) (Smyth et al. 1990). In monocots, such as grasses, the floral architecture is distinct from that of eudicots (**Fig. 1B**). The spikelet is the primary unit of the inflorescence and comprises glumes (bract-like organs) and florets that lack sepals and petals (**Fig. 1B**). The number of florets in the spikelet varies among grass species. In rice, one spikelet contains a fertile floret and a pair of sterile lemmas (also known as empty glumes). The rice floret consists of a pair of bract-like organs (lemma and palea), two lodicules (equivalent to eudicot petals) in whorl 2, six stamens in whorl 3 and two carpels forming a pistil in whorl 4 . In Arabidopsis flowering, the shoot apical meristem converts into the inflorescence meristem (IM), which continuously produces the floral meristems (FMs) at lateral regions. During rice reproductive development, the IM initiates the primary branch meristems, followed by the secondary branch meristems, spikelet meristems and finally the FMs (**Fig. 1C**).

The genetic ABC model was introduced in 1991 based on studies of floral homeotic mutants in Arabidopsis and

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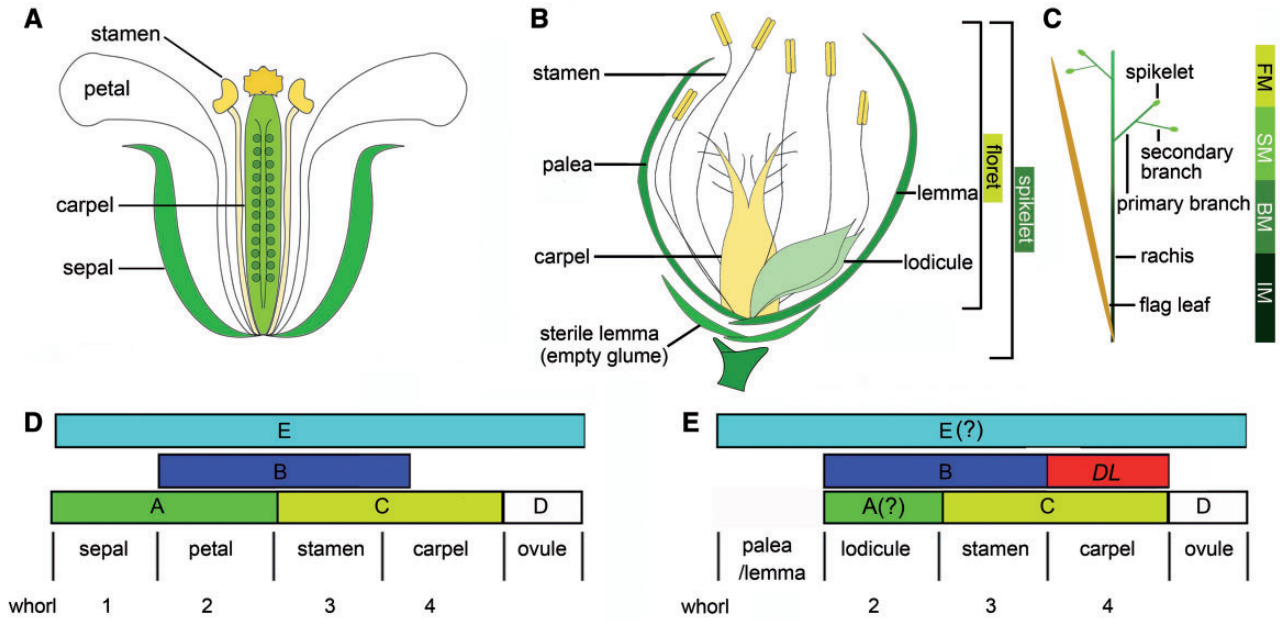

Fig. 1 Schematic representation of Arabidopsis and rice flowers and the genetic models of floral organ identity and determination in Arabidopsis and rice. (A) Arabidopsis flowers contain four concentric whorls of floral organs. From the outermost to innermost, these include: whorl 1, four sepals; whorl 2, four petals; whorl 3, six stamens; and whorl 4, two carpels. (B) Rice flowers are also composed of four concentric whorls of floral organs. From the outermost to innermost, these include: whorl 1, one palea and one lemma; whorl 2, two lodicules; whorl 3, six stamens; and whorl 4, one carpel. (C) Structure of the rice inflorescence. (D) The revised Arabidopsis ABC model. A-class genes, *APETALA1* (*AP1*) and *AP2*; B-class genes, *AP3* and *PISTILLATA* (*PI*); C-class gene, *AGAMOUS* (*AG*); D-class genes, *SEEDSTICK* (*STK*), *SHATTERPROOF1* (*SHP1*) and *SHP2*; and E-class genes, *SEPALLATA1* (*SEP1*), *SEP2*, *SEP3* and *SEP4*. (E) The rice organ identity model. B-class genes, *OsMADS2*, *OsMADS4* and *OsMADS16*; C-class genes, *OsMADS3* and *OsMADS58*; D-class gene, *OsMADS13*; and E-class genes, *OsMADS1*, *OsMADS5*, *OsMADS7*, *OsMADS8* and *OsMADS34*. *DL*, *DROOPING LEAF*.

Antirrhinum majus (Coen and Meyerowitz 1991, Ito 2011). Floral organ identity is determined by the combinatorial action of floral ABC-class homeotic proteins. Later, the ABC model was expanded to include the fourth and fifth classes: the D- and E-class genes (**Fig. 1E**). The E-class quadruple *sep1 sep2 sep3 sep4* mutant plants show all floral organs being transformed into leaves (Ditta et al. 2004). The E-class SEPALLATA (SEP) proteins form larger homo- and hetero-oligomeric complexes with A-, B-, C- and D-class proteins to specify the floral organ identities (Honma and Goto 2001, Jetha et al. 2014). Based on the quartet model, the A- and E-class complex [APETALA1 (AP1)–SEP] specifies the sepal identity; A-, B- and E-class proteins [AP1–SEP–AP3–PISTILLATA (PI)] specifies petals; the B-, C- and E-class complex [AGAMOUS (AG)–SEP–AP3–PI] specifies stamens; the C- and E-class complex (AG–SEP) specifies carpels; and the D- and E-class complex [SEEDSTICK (STK)–SEP] specifies ovules (Yanofsky et al. 1990, Jack et al. 1992, Mandel et al. 1992, Goto and Meyerowitz 1994, Honma and Goto 2001, Mendes et al. 2013). Moreover, E-class genes also function upstream of B- and C-class genes to regulate their expression (Kaufmann et al. 2009), possibly representing auto- and cross-regulation of the MADS proteins. Although SEP1–SEP4 generally function redundantly, SEP3 genetically has major functions. While *sep1 sep2 sep3* shows strong defects like B/C-class double mutants, *sep1 sep2 sep4* is phenotypically normal (Ditta et al. 2004). SEP1–SEP4 heterotetramer proteins have distinct binding properties to CArG-box pairs in vitro (Jetha et al. 2014). SEP3 shows binding to a larger range of distances between the CArG-boxes and thus presumably to a wider spectrum of target genes.

The ABC model basically holds true for reproductive development in rice; however, it remains unclear whether true A-class genes exist that determine the identity of the first- and second-whorl organs (Yoshida and Nagato 2011, Tanaka et al. 2013, Zhang and Yuan 2014). Further, the identities of the lemma and palea are controversial and are often considered to be non-floral bract- and prophyll-like organs, respectively. Rice tends to have duplicated BCDE-class genes derived from ancestral gene duplication events (Hirano et al. 2014). For example, there are two *PI* homologs, two AG homologs and five *SEP*-like genes in rice [*OsMADS1* and *LEAFY HULL STERILE1* (*LHS1*), *5*, *7*, *8* and *34*] (**Fig. 1E**) (Yamaguchi et al. 2006, Hirano et al. 2014). These duplicated genes are partially redundant but have functional diversifications based on their own expression patterns. Whether E-class functions are consevered in rice is controversial (Hirano et al. 2014). Independently of C-class genes, one YABBY type transcription factor, DROOPING LEAF (DL), plays an important role in specifying carpel identity and meristem determinacy. *DL* is mainly expressed in the presumptive region of carpel initiation in the FM and in the carpel primordia. The carpels of *dl* mutants homeotically transform into stamens in accordance with the expansion of B-class gene expression (**Fig. 1E**) (Yamaguchi et al. 2004).

Functional Specificity of Floral Homeotic Proteins

Overexpression of ABC genes was performed to assess the robustness of the ABC model with respect to its effect on floral organ identities (Jack et al. 1992, Mizukami and Ma 1992, Goto and Meyerowitz 1994). These experiments suggested that each class maintains functional specificity and can sufficiently induce downstream events when overexpressed. Chimeric domain-swapping analyses of ABC MADS proteins revealed that the MADS domains themselves are interchangeable. For example, the specificity of AP1 and AG is linked to the C-terminal region of the MADS domain and the I-domain [Intervening domain between MADS and the keratin-like (K) domain], while the specificity of AP3 and PI is linked to the I-domain and K-domain (Krizek and Meyerowitz 1996). These results indicate that functional specificity is conferred by protein complexes rather than the DNA binding specificity of individual proteins. A recent immunopurification assay of the whole complex revealed that SEP3 forms a complex of approximately 670 kDa, which is >10-fold greater than the predicted molecular weight of the SEP3 dimer (Smaczniak et al. 2012). MADS proteins assemble to form complexes with chromatin-remodeling factors including the SWI/SNF ATPases BRAHMA (BRM) and SPLAYED (SYD), the CHD remodeler PICKLE (PKL), the transcriptional co-repressors SEUSS (SEU) (Tamada et al. 2009) and LEUNIG-HOMOLOG (LUH), the histone demethylase RELATIVE OF EARLY FLOWERING 6 (REF6), and the ISWI-type remodelers CHROMATIN REMODELING 4 (CHR4), CHR11 and CHR17 (Smaczniak et al. 2012). Still, very little is known about functional multimeric complexes that specify specific cell types in each floral organ.

Mode of Action of Floral Homeotic Proteins

The mechanism by which ABC floral homeotic proteins control flower development has remained unknown for a long time. The homeotic genes are continuously expressed after organ identity is specified. The use of efficient inducible systems for ABC protein expression has shown that the homeotic genes control various aspects throughout the flower development. In the *ag-1 35S::AG-GR* line with inducible AG activity (a constitutive promoter-driven AG gene fused with a steroid-binding domain of the rat glucocorticoid receptor), a single dexamethasone treatment led to the nuclear accumulation of the AG–GR fusion protein for 2–3 d, resulting in the formation of leaf-like laminar stamens (Ito et al. 2004, Ito et al. 2007). To produce normal mature stamens, prolonged AG activity from stage 5–6 up to stage 10 is necessary. AG can induce normal stamens from organs originally fated to be petals at stage 5–6. However, if AG was induced after stage 7, microsporogenesis (pollen formation) was no longer induced, but petals had stalks, indicating that some late target genes of AG can be induced independently of early targets.

The initial AG expression starting from stage 3 is activated by the homeobox gene *WUSCHEL* (*WUS*) and the floral identity gene *LEAFY* (*LFY*) (Lenhard et al. 2001, Lohmann et al. 2001). For floral stem cell regulation, it is reported that AG may recruit CURLY LEAFY (CLF), a Polycomb group (PcG) protein on *WUS* from stage 3 for *WUS* repression (Liu et al. 2011) . However, the direct repression of *WUS* by AG is very mild because *WUS* is not fully terminated until stage 6 (Lenhard et al. 2001, Lohmann et al. 2001), and *35S::AG* lines still produce normal carpels (Mizukami and Ma 1992). Through direct induction of the C2H2 zinc finger repressor KNUCKLES (KNU), AG terminates *WUS* more effectively (Sun et al. 2009). In stage 6, AG induces *KNU*, which in turn terminates *WUS* expression. From stage 3 to stage 6, AG induces *KNU* over a 2 d period. This 2 d induction is timed by cell division-associated dilution of H3K27me3 on *KNU* chromatin, which is caused by the eviction of PcG protein from *KNU* PRE (Polycomb-Responsive Element-like element) by AG binding at the same site (Sun et al. 2014).

When the AG activity was continuously induced in stage 3 floral primordia of *ag-1 35S::AG-GR*, the flower showed carpelloid sepals in whorl 1, a reduced number of mature stamens in whorls 2 and 3, and carpels in whorl 4. When AG was induced at stage 4 (with only 1 d delay from stage 3 under 24 h light conditions) or later, the flower showed carpelloid sepals in whorl 1, ten stamens in whorls 2 and 3, four carpelloid sepals in whorl 4, ten stamens in whorls 5 and 6, and carpels in whorl 7 due to partial meristem indeterminacy. In the line with inducible RNA interference (RNAi) for AG, knockdown of AG at the middle stages of flower development led to branched-trichome formation on the surface of carpels. These results indicate that AG induces various targets throughout reproductive development, and further that AG represses leaf-specific genes in reproductive organs.

Downstream Targets of Floral Homeotic Proteins

The availability of expression profiling methods and the inducible lines has allowed the time-lapse analyses of downstream genes. Chromatin immunoprecipitation (ChIP) assays followed by quantitative PCR, tiling array screening or high-throughput sequencing have enabled the identification of direct target sites. Combined analyses of expression and genome-wide binding of the key floral transcription factors provide a holistic view of transcriptional networks. To date, whole genome-wide target analyses have been carried out for the ABCE-class transcription factors, AP1, AP2, AP3/PI, AG and SEP3 in addition to LFY (Kaufmann et al. 2009, Kaufmann et al. 2010, Yant et al. 2010, Winter et al. 2011, Wuest et al. 2012, O'Maoileidigh et al. 2013). The general finding of these genome-wide analyses was that floral transcription factors bind to a very large number of target sites (~1,500 for LFY and AP3/PI; ~2,000 for AP1, AP2 and AG; and ~4,000 for SEP3), and a limited portion of the bound genes exhibit expression changes in the presence/absence of the respective transcription factors. Generally speaking, the genetic combinatorial model has been supported by the target analyses. Over 60% of the genes bound by AP1 are also bound by SEP3 (Kaufmann et al. 2010). It will be interesting to determine

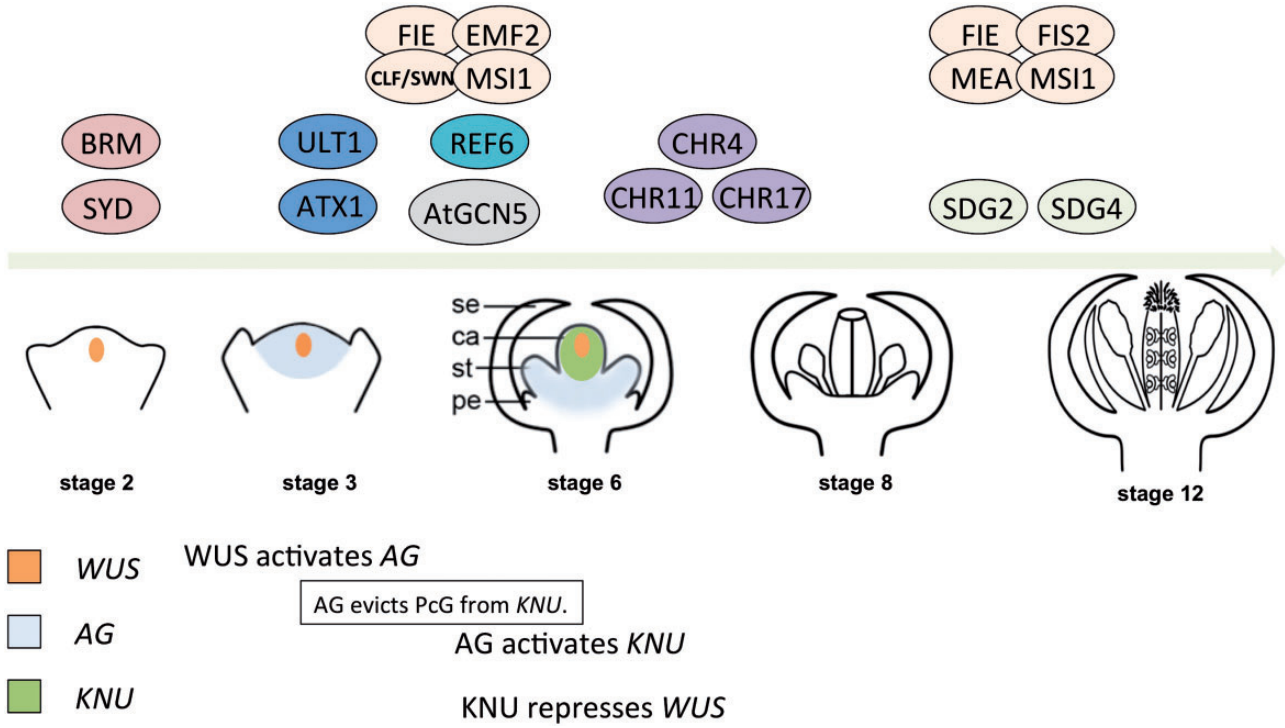

Fig. 2 Chromatin-remodeling factors in flower development and floral stem cell regulation. During flower development, various chromatin-remodeling factors modulate gene expression. In floral stage 1–2 (Smyth et al. 1990), the expression of floral homeotic B- and C-class genes is prevented by the EMF2–PRC2 complex. To reverse the repressive effects of Polycomb-mediated H3K27me3 repressive marks, LFY and SEP3 recruit the SWI/SNF chromatin-remodeling factors SYD and BRM to *AG* and *AP3* regulatory loci for their activation. Meanwhile, the trxG protein ULT1 interacts with ATX1 for the activation of *AG* and other MADS box genes. Beginning in floral stage 3, when the MADS box genes are induced, the chromatin-remodeling factors CHR4, 11 and 17 interact and form large complexes with AP1, PI, AP3, AG and SEPs. The JmjC-domain protein REF6, the demethylase of H3K27me3, interacts with AG and SEP3 to promote chromatin opening and facilitate AG, inducing the transcription of many downstream targets for the proper development of stamens and carpels. During male and female gametophyte development, SDG2, an H3K4 methyltransferase, may function in gene activation. In contrast, the FIS2–PRC2 complex plays a role in gene silencing during gametogenesis and seed development. In addition, SDG4, an H3K36 methyltransferase, is involved in pollen tube formation. For floral stem cell regulation, *AG* is activated by WUS and LFY from stage 3. It is known that AG may directly repress *WUS* from stage 3 by recruiting PcG to *WUS*. However, the direct repression of *WUS* by AG is mild because *WUS* is not fully terminated until stage 6. Through direct induction of the C2H2 zinc finger repressor KNU, AG terminates *WUS* more effectively in an indirect manner. In stage 6, AG induces *KNU*, which in turn shuts off *WUS* expression. From stage 3 to stage 6, AG induces *KNU* over a 2 d period. This 2 d induction is timed by cell division-associated dilution of H3K27me3 on *KNU* chromatin, which is caused by the eviction of PcG from *KNU* PRE by AG binding at the same site. In the AG/WUS regulatory pathway, the acetyltransferase AtGCN5 may function to regulate the proper expression patterns of both *AG* and *WUS*.

whether AP1 has SEP3-independent functions and whether SEP3 has AP1- and AG-independent functions. Analyses of the target genes of AP1, SEP3 and AG with high fidelity will help to answer these questions.

Floral homeotic proteins regulate many different types of genes, including transcription factors, hormone biosynthesis and signaling genes, and genes involved in cell growth and structure. The expression of each target gene is regulated in a cell-type-specific manner at precise stages of flower development. For example, AG directly induces the transcription of the SPOROCYTLESS/NOZZLE (SPL/NZZ) and KNU transcription factors at stage 6 in anther primordia to induce microsporogenesis and in FMs to terminate floral stem cell activities by repressing the stem cell-specifying gene *WUS*, respectively (Sun et al. 2009, Sun et al. 2014). In *ag-1 35S::AG-GR*, *SPL/NZZ* was induced within a few hours after the AG induction, while *KNU* started to be induced after a 2 d time lag (Sun et al. 2009, Sun et al. 2014). *SPL/NZZ* was detected in presumptive pollen sacs in the organ primordia of the *ag* mutant flowers only in certain developmental stages (Ito et al. 2004). This indicates that the transcriptional induction of *SPL/NZZ* depends on stage- and cell-type specific factors, which are developmentally regulated in an AG-independent manner. Therefore, AG induction in flowers at certain-stages (5–6) led to rapid induction of *SPL/NZZ*. In contrast, *KNU* induction depends on the cell-division-dependent changes of histone modification triggered by AG (**Fig. 2**) (Sun et al. 2009, Sun et al. 2014). AG binding sites on the *KNU* promoter are necessary for Polycomb recruitment (see the section 'H3K27 methylation and the Polycomb group complex) and the binding of AG causes the eviction of PcG from *KNU*, which leads to the delayed induction of *KNU*, associated with cell division-dependent dilution of the repressive status.

Additionally, AG induces the jasmonic acid (JA) biosynthetic gene *DELAYED ANTHER DEHISCENCE 1* (*DAD1*) after stage 10 in

developing stamen filaments (Ito et al. 2007). JA controls stamen maturation; filament elongation, anther opening and pollen maturation. A laminar stamen produced after temporal induction of *AG* is interpreted as an organ which has had *SPL/NZZ* expression but lacked stamen maturation genes including *DAD1*. In contrast, a petal with a stalk is an organ that has had the maturation genes but lacked *SPL/NZZ* expression. AP3/PI also regulates different targets in a stage-specific manner, including almost 1,000 genes in the early floral stages and approximately 500 different sets of genes during late flower development (Wuest et al. 2012).

Global profiling of target analysis was also carried out for the rice *SEP*-like gene *OsMADS1*. *OsMADS1* directly represses the expression of another *SEP*-like gene, *OsMADS34*, and various transcription factors, including class III homeodomain-leucine zipper member (OsHB4), BEL1-like member (OsBLH1), OsKANADI2 and OsKANADI4 (Khanday et al. 2013).

Epigenetic Regulation of Genes Located Upstream and Downstream of Floral Homeotic Protein-Encoding Genes

Epigenetic regulation is defined as heritable changes that are not caused by changes in the DNA sequence but rather by DNA methylation or histone modification, and these changes play key roles in flower development. Of the various histone modifications, histone lysine methylation is well studied and changes dynamically during flower development (Gan et al. 2013). Histone methylations can be generally divided into activating marks [the methylation of histone H3 lysine 4 (H3K4) and lysine 36 (H3K36)] and repressive marks [the methylation of histone H3 lysine 9 (H3K9) and lysine 27 (H3K27)] (Pien and Grossniklaus 2007, Gan et al. 2013). Antagonizing the establishment of histone methylation, lysine-specific demethylase1 (LSD1)- and Jumonji-C (JmjC)-domain proteins function to demethylate histones. In this section, their functions and histone-modifying enzymes in flower development are discussed (**Table 1**).

H3K9 methylation

SUVH4/KRYPTONITE (KYP) is an H3K9 histone methyltransferase (HMT) initially identified in a suppressor screen of the *superman* (*sup*) epi-alleles [the *clark kent* (*clk*) alleles], which have excessive cytosine methylation at the *SUP* locus (Jacobsen 1997). The phenotype of *clk* was rescued in the *kyp* mutant. As a repressive mark, H3K9me2 in Arabidopsis is associated with CpG DNA methylation and seems to be heterochromatin specific (Mathieu et al. 2005).

H3K9 methylation also influences floral organ maturation in rice. A rice homolog of *Su(var)3-9* is the *SET DOMAIN GROUP 728* (*SDG728*) H3K9 HMT. In the *SDG728* knockdown lines, seed size and weight were reduced, and the activities of a *Ty1-copia* element and *Tos17* retrotransposons were activated (Qin et al. 2010).

There are 21 JMJ proteins in both Arabidopsis and rice, which can be divided into five groups (Groups I, II, III, IV and V) (Sun and Zhou 2008). In rice, T-DNA insertion mutants of the histone H3K9 demethylase *JMJ706* affect spikelet development, including altered floral morphology and organ number (Sun and Zhou 2008). JMJ706 regulates the expression of *OsMADS47* and *DEGENERATED HULL1* (*DH1*), a putative lateral organ boundary-expressed transcription factor required for rice rudimentary glume formation. In the *jmj706* mutant, the expression of *OsMAD47* and *DH1* is reduced, which is associated with increased levels of H3K9me2/3 at the promoter and 5′ regions of *OsMAD47* and *DH1* (Sun and Zhou 2008).

H3K27 methylation and the Polycomb group complex

H3K27me3 is known as a repressive histone mark responsible for gene silencing at various developmental stages in both animals and plants. In Arabidopsis, H3K27me3 is catalyzed by PcG protein-containing complexes (Lafos et al. 2011). It has been found that Arabidopsis PcG comprises two subgroups: Polycomb Repressive Complex 1 (PRC1) and PRC2. Corresponding to *Drosophila* PRC2 components, which include extra sex comb (ESC), enhancer of zeste [E(Z)], suppressor of zeste 12 [SU(Z)12] and p55, Arabidopsis PRC2 has one ESC homolog [FERTILIZATION INDEPENDENT ENDOSPERM (FIE)]; three E(Z) homologs [CLF, SWINGER (SWN) and MEDEA (MEA)]; three SU(Z)12 homologs [VERN (VRN2), FERTILIZATION INDEPENDENT SEED2 (FIS2) and EMBRYONIC FLOWER 2 (EMF2)]; and five p55 homologs [MULTICOPY SUPPRESSOR OF IRA1–5 (MSI1–MSI5] (Pien and Grossniklaus 2007). At different developmental stages, these PRC2 proteins may form different heterocomplexes. The FIS complex, containing MEA/SWN, FIS2, FIE and MSI1, functions to silence target genes during early seed development and gametogenesis. The VRN complex, containing CLF/SWN, VRN2 and FIE, functions during vegetative development and the floral transition, whereas the EMF complex, containing FIE, MSI1, CLF/SWN and EMF2, functions during inflorescence development and flower organogenesis (Pien and Grossniklaus 2007).

In Arabidopsis, thousands of genes are regulated by the repressive mark H3K27me3, which is enriched in the transcribed regions (Zhang et al. 2007). Among these genes, a significant number are involved in transcriptional regulation for many developmental processes. In flower development, H3K27me3 targets floral-specific genes such as *AP3*, *PI*, *AG* and *SUP*. It is known that H3K27me3 is deposited by PcG; however, it is unclear how PcG is recruited to specific targets. The ASYMMETRIC LEAVES1 (AS1)–AS2 complex recruits PcG to *BREVIPEDICELLUS* (*BP*) and *KNOTTED-LIKE FROM ARABIDOPSIS THALIANA 2* (*KNAT2*) via direct interaction with FIE and CLF to silence these two genes in differentiating leaves (Lodha et al. 2013). During the floral transition, the key floral repressor *FLOWERING LOCUS C* (*FLC*) also needs to be silenced. Within the *FLC* locus, a PRE was identified in the region near the transcription start site (TSS) and the long first intron (Buzas et al. 2012). This PRE is reported to be involved in the transcriptional silencing of *FLC* expression. Discovered first in

Table 1 List of chromatin factors involved in Arabidopsis and rice flower development

Family	Name	Gene number	Molecular function	References
SWI/SNF2 type ATP-dependent chromatin remodelers	BRAHMA (BRM)	At2G46020	Interact with SYD, AP1 and SEP3 to form a complex to activate B- and C-class genes	Hurtado et al. (2006); Bezhani et al. (2007); Wu et al. (2012)
	SPLAYED (SYD)	At2G28290	Interact with SYD, AP1 and SEP3 to form a complex to activate B- and C-class genes	Wagner and Meyerowitz (2002); Kwon et al. (2005); Bezhani et al. (2007); Walley et al. (2008); Wu et al. (2012)
	CHROMATIN REMODELING 4 (CHR4)	At5G44800	Interact with AP1, AP3, PI, AG and SEP3 to form a large complex	Smaczniak et al. (2012); Li et al. (2014)
	CHROMATIN REMODELING 17 (CHR17)	At5G18620	Interact with AP1, AP3, PI, AG and SEP3 to form a large complex	Smaczniak et al. (2012); Li et al. (2014)
	CHROMATIN REMODELING 11 (CHR11)	At3G06400	Interact with AP1, AP3, PI, AG and SEP3 to form a large complex	Smaczniak et al. (2012); Li et al. (2014)
	PICKLE (PKL)	At2G25170	Control apical dominance, flowering, anther dehiscence and carpel polarity; repress embryonic traits during germination	Eshed et al. (1999); Henderson et al. (2004); Smaczniak et al. (2012; Zhang et al. (2014)
H3K27me3 demethylases	RELATIVE OF EARLY FLOWERING 6 (REF6)	At3G48430	H3K27me3-specific demethylase, component of the large complex containing AP1, AG and SEP3	Lu et al. (2011); Smaczniak et al. (2012)
Polycomb group (PcG) proteins	FERTILIZATION-INDEPENDENT ENDOSPERM (FIE)	At3G20740	Component of PRC2, WD40 motif-containing protein	Pien and Grossniklaus (2007)
	EMBRYONIC FLOWER 2 (EMF2)	At5G51230	Component of PRC2, VEFS domain-containing protein	Pien and Grossniklaus (2007)
	MULTICOPY SUPPRESSOR OF IRA1 (MSI1)	At5G58230	Component of PRC2, WD40 motif-containing protein	Pien and Grossniklaus (2007)
	CURLY LEAF (CLF)	At2G23380	Component of PRC2, H3K27me3 methyltransferase, involved in floral organ development	Pien and Grossniklaus (2007)
	SWINGER (SWN)	At4G02020	Component of PRC2, H3K27me3 methyltransferase, involved in floral organ development	Pien and Grossniklaus (2007)
	FERTILIZATION INDEPENDENT SEED 2 (FIS2)	At2G35670	Component of PRC2, homolog of Suppressor of zeste 12 [SU(Z)12], involved in seed development	Pien and Grossniklaus (2007)
H3K4 methyltransferases	HOMOLOG of TRITHORAX (ATX1)	At2G31650	H3K4 methyltransferase, recruited by ULT1 for AG activation	Alvarez-Venegas et al. (2003); Saleh et al. (2008)
	SET DOMAIN GROUP 2 (SDG2)	At4G15180	H3K4 methyltransferase, functions for gene activation during male and female gametogenesis	Berr et al. (2010)
H3K36 methyltransferases	SET DOMAIN GROUP 4 (SDG4)	At4G30860	H3K36 methyltransferase, involved in pollen tube formation	Thorstensen et al. (2008)
	SET DOMAIN GROUP 8 (SDG8)	At1G77300	H3K36 methyltransferase, involved in floral organ development and gametogenesis	Xu et al. (2008); Cazzonelli et al. (2009); Grini et al. (2009); Berr et al. (2010); Xu et al. (2015)
MADS transcription factors	AGAMOUS (AG)	At4G18960	C-class floral MADS-domain protein, evictor of PcG on KNU chromatin	Sun et al. (2014)
	SEPALLATA3 (SEP3)	At1G24260	E-class floral MADS-domain protein, recruiter of SYD and BRM for AG and AP3 activation	Wu et al. (2012)
	LEAFY (LFY)	At5G61850	Homeotic protein for floral induction, recruiter of SYD and BRM for AG and AP3 activation	Wu et al. (2012)
SAND-domain factors	ULTRAPETALA1 (ULT1)	At4G28190	TrxG group protein, antagonist of PcG and interactor with ATX1	Carles and Fletcher (2009)
WD40 repeats	TOPLESS (TPL) ABERRANT SPIKELET AND PANICLE1 (ASP1)	At1G15750 Os08g06480	Embryonic axis specification; cofactor in repressing ARRs, FT, B-, C- and E-class genes. Meristem specification and auxin response	Leibfried et al. (2005); Kieffer et al. (2006); Tamada et al. (2009); Dinh et al. (2012); Krogan et al. (2012); Yoshida et al. (2012)
Histone H3K9 methyltransferase	SET DOMAIN GROUP 728 (SDG728)	Os05g41172	Repress a *Ty1-copia* element and *Tos17* retrotransposons in seed development	Qin et al. (2010)
Histone H3K36 methyltransferase	SET DOMAIN GROUP 725 (SDG725)	Os02g34850	Regulate brassinosteroid-related genes	Sui et al. (2012)
Polycomb group proteins (PcG)	EMBRYONIC FLOWER 2 (OsEMF2b)	Os09g13630	Regulate E-class genes (OsMADS1 and OsMADS6) in flowering and floral organ identity control	Luo et al. (2009); Conrad et al. (2014)
JmjC domain-containing proteins	JUMONJI706 (JMJ706)	Os10g42690	Regulate *OsMAD47* and *DH1*	Sun and Zhou (2008)

Drosophila, the PRE is responsible for the recruitment of PcG to specific genes, possibly through DNA-binding proteins or non-coding RNAs (Sawarkar and Paro 2010, Simon and Kingston 2013). In contrast, the histone demethylases JMJ30 and JMJ32 are able to demethylate H3K27me3 at the *FLC* locus, thereby dampening its repression (Gan et al. 2014). In another example, it was found that a different 50 bp sequence located in the promoter region of *LEAFY COTYLEDON2* (*LEC2*) (Berger et al. 2011), a master regulator of seed development, may function as a putative PRE. Referred to as Repressive *LEC2* Element (RLE), this fragment was necessary for the silencing of *LEC2* by H3K27me3. When this 50 bp *RLE* sequence was introduced into the *FLAVANONE 3 HYDROXYLASE* (*F3H*) promoter, the *pF3H::GUS* reporter was silenced. Evidence for the existence of an Arabidopsis PRE is further supported by the existence of a 153 bp PRE-like sequence located in the promoter region of *KNU* (approximately 1 kb upstream of the *KNU* TSS) (Sun et al. 2014). Similarly, when this 153 bp fragment was inserted in the *F3H* promoter, the reporter activity of *pF3H::YFP* was silenced.

PcG-mediated H3K27me3 also plays a very important role in rice. Some rice homologs of PRC2 components have been studied, but only a T-DNA insertion mutant of *OsEMF2b* [a homolog of Su(z)12] showed altered flowering time and defective floral organs, including short panicles, anther indehiscence and multiple indeterminate ovaries (Luo et al. 2009). This phenotype was similar to those of some E-class gene mutants (*osmads1* and *osmads6*), which is consistent with the down-regulation of *OsMADS1* and *OsMADS6* in *emf2b*. This finding indicates that genes upstream of *OsMADS1* and *OsMADS6* are repressed by H3K27me3. Therefore, PRC2 may function in rice floral meristem determinacy through indirect regulation of the expression of SEP-like genes (Luo et al. 2009, Conrad et al. 2014). Rice T-DNA insertion mutants of other components of the PRC2 complex have no obvious phenotype, possibly due to genetic redundancy (Luo et al. 2009).

H3K4 methylation and the trithorax group complex

The histone modification H3K4me3 marks active chromatin. In Arabidopsis, H3K4me3 is catalyzed by trithorax group (trxG) proteins and predominantly accumulate in promoters and 5′ genic regions (Zhang et al. 2009). A well-studied trxG protein, ULTRAPETALA1 (ULT1), functions partially to induce *AG* in floral stem cells (Carles and Fletcher 2009). ULT1 has a SAND domain, which directly binds to *AG* regulatory sequences. Via direct interaction with another trxG component, ATX1/SDG27, ULT1 counteracts the PcG-repressive activity of CLF to modulate the H3K4 methylation status at the *AG* locus. *ATX1/SDG27* encodes an H3K4 HMT in Arabidopsis (Alvarez-Venegas et al. 2003). The null *atx1/sdg27* mutant exhibits homeotic conversion of floral organs, suggesting that *ATX1/SDG27* is also involved in floral organ identity. In *atx1/sdg27* mutants, lower expression levels of floral homeotic genes, including *AP1*, *AP2*, *AP3*, *PI* and *AG*, are observed, indicating that trxG has a positive role in floral organ identity control.

In addition to ULT1 and ATX1/SDG27, several other SDG proteins have also been reported to be H3K4 HMTs (Kim 2005, Saleh et al. 2008, Berr et al. 2009, Tamada et al. 2009, Berr et al. 2010). Among these SDG genes, the *sdg2* mutant displays a pollen and ovule sterility phenotype, although no floral organ identity defects are observed (Berr et al. 2010). Noticeably, in the *sdg2* mutant, the levels of H3K4me3 on *SPL/NZZ*, *BTB AND TAZ DOMAIN PROTEIN 3* (*BT3*) and *MSI1* loci are significantly decreased, indicating the important role of trxG in proper gametophytic development. AG is essential for the direct induction of *SPL/NZZ* (Ito et al. 2004). It is interesting to note that AG is involved in the changes in H3K4me3 status at the *SPL/NZZ* locus. Another SDG gene, *SDG4*, plays an important role in pollen tube growth (Thorstensen et al. 2008). In the *sdg4* mutant, pollen tubes grow much more slowly than those in wild-type plants, leading to severe male sterility. This finding indicates that SDG4 is capable of modulating the expression of genes that function in the growth of pollen tubes (Cartagena et al. 2008).

H3K36 methylation

H3K36me3, which enriches in the 5′ region of transcribed regions of genes (Roudier et al. 2011), marks active chromatin. The HMTs SDG7 and SDG8/ASHH2 are responsible for H3K36 methylation, the loss of which leads to pleiotropic developmental defects including floral organ abnormalities and gametophytic defects (Xu et al. 2008, Cazzonelli et al. 2009, Grini et al. 2009, Berr et al. 2010, Xu et al. 2015). *sdg8/ashh2* flowers display homeotic conversions such as sepal to carpel, petal to stamen and carpelloid organs, all of which might be due to spreading of the *AG* expression domain into whorls 1 and 2, in accordance with down-regulation of negative regulators of *AG* in *sdg8/ashh2*. Moreover, ovule and stamen development are also obviously affected (Grini et al. 2009), which is due to a substantial decrease in H3K36me3 at *MYB99* and *AtDMC1* loci, which are involved in embryo sac and pollen development, respectively. In rice, knockdown of the H3K36 HMT *SDG725* causes pleiotropic developmental defects, including dwarfism, erect leaves, and reduced spikelets and rachis branches (Sui et al. 2012).

Histone Acetylation

Histone acetylation is another indicator of an active genetic locus. There are multiple histone acetyltransferases (HATs) and histone deacetylases (HDAs) that add or remove acetyl groups on histones, respectively, in Arabidopsis (Pandey et al. 2002). One of the HATs, *AtGCN5*, is reported to be involved in multiple developmental processes (Bertrand et al. 2003). In the *atgcn5* mutant, the *WUS* expression domain is expanded beyond the organizing center, resulting in global defects in vegetative development. In addition to its roles in vegetative development, *AtGCN5* is further suggested to be involved in floral stem cell regulation. Terminal flowers are produced in *atgcn5* mutant plants, and the mutant flowers display homeotic transformation of petals into stamens and sepals into

filamentous structures. Ectopic carpels are also observed in *atgcn5* mutant flowers. These phenotypes could be attributed to the expansion of the expression domains of *AG* and *WUS*, suggesting that *AtGCN5* is required for the induction of negative regulators for *AG* and *WUS* (Bertrand et al. 2003).

Antagonizing the effect of HATs, *AtHD1/HDA19* is known to form a complex with *LUG–SEU* for the regulation of *AG* expression via removal of the acetylation mark from the *AG* locus (Tian and Chen 2001, Chen and Tian 2007). By repressing *AG* in whorl 1 and whorl 2, the *LUG–SEU–HDA19* complex maintains *AG* expression in the correct domain. In *lug seu* single or double mutants, *AG* is ectopically expressed throughout all floral organs, leading to homeotic conversion of sepals and petals into reproductive organs. HDA19 was also recently found to interact with AP2 and TOPLESS (TPL) (see below) for negative regulation of floral homeotic genes (Krogan et al. 2012).

Chromatin Remodeling Factors

In addition to the protein factors and complexes directly responsible for histone modification, other chromatin-remodeling factors and chromatin structural proteins also have indispensable roles in plant growth, including flower development. Here, their cross-talk and indirect roles in histone modification are discussed (**Table 1**).

GIANT KILLER and transposable element silencing via AT-HOOK

The nuclear matrix attachment regions are AT-rich DNA sequences and contribute to functional nuclear architecture in plants and animals (Cai et al. 2003, Ng et al. 2009). A series of matrix proteins with AT-hook DNA-binding motifs have been shown to bind to the DNA minor groove of the AT-rich MAR target sites, affecting the epigenetic state of target genes through direct structural changes in chromatin and/or recruitment of chromatin modifiers, such as the mammalian histone deacetylase 1 (HDAC1) (Cai et al. 2003, Han et al. 2008). The Arabidopsis genome contains AT-HOOK MOTIF NUCLEAR-LOCALIZED PROTEIN 1–29 (AHL1–29), some of which have been characterized (Matsushita et al. 2007, Ng et al. 2009, Xu et al. 2013, Xu et al. 2015). *AHL21/GIANT KILLER* (*GIK*), as a target of the floral homeotic protein AG, negatively regulates multiple genes downstream of AG, partially through the repressive histone modification H3K9me2. The direct GIK target genes include several key transcriptional regulators of organ patterning and differentiation during reproductive development, such as *ETT/ARF3* (Ng et al. 2009). GIK fine-tunes the expression of multiple targets of AG. Another AHL protein, AHL22, interacts with HDACs, and overexpression of AHL22 suppresses the expression of flowering activator *FLOWERING LOCUS T* (*FT*), resulting in a late-flowering phenotype (Yun et al. 2012). *AHL16/TRANSPOSABLE ELEMENT SILENCING VIA AT-HOOK* (*TEK*) was found to maintain genome integrity by silencing transposable elements and repeat-containing genes (Xu et al. 2013). TEK has a role in the maintenance of DNA methylation and histone deacetylation by interacting with Retinoblastoma-associated protein 46/48, FVE and MSI5 (Xu et al. 2013). TEK is also important for pollen wall formation, and loss of function of *tek* leads to male sterility due to the absence of nexine (Xu et al. 2013, Lou et al. 2014).

MORF-RELATED GENE 1 and 2

MORF-RELATED GENE 1 and 2 (MRG1/2) proteins have recently been found to bridge the two important histone modifications for proper transcription of target genes (Xu et al. 2015). MRG1/2 are Arabidopsis homologs of the highly conserved MRG15 (MORF4-related gene on chromosome 15) proteins. They contain a chromodomain at their N-termini, which is able to bind to H3K36me3 and recruit the HATs HISTONE ACETYLTRANSFERASE OF THE MYST FAMILY 1 and 2 (HAM1/2) to achieve 2-fold hypertranscription by increasing the histone acetylation level of target loci (Xu et al. 2015). The study mainly focused on the flowering time genes, which show quantitative effects in timing of flowering, and loss-of-function mutants did not have obvious phenotypes in reproductive development. However, because H3K36me3 is the prevalent mark for transcription and the *sdg8* mutant showed defects in floral organs, it is still possible that MRG1/2 may have fine-tuning roles in the transcriptional regulation of flower development genes.

SWI/SNF ATPases

SWI/SNF ATPases are important catalytic subunits involved in chromatin opening and transcription facilitation (Flaus et al. 2006, Hurtado et al. 2006, Bezhani et al. 2007, Wu et al. 2012). Arabidopsis contains four members of the SWI/SNF subfamily: SYD, BRM, CHR12 and CHR23. Double *chr12* and *chr23* mutants are embryonic lethal, while single mutants are indistinguishable from the wild type (Sang et al. 2012). The absence of either *SYD* or *BRM* caused pleiotropic developmental defects, including reduced petals and stamens, female sterility and reduced anther dehiscence (Wagner and Meyerowitz 2002, Kwon et al. 2006). The *brm* mutant also exhibited a unique root defect along with male sterility (Wagner and Meyerowitz 2002, Hurtado et al. 2006). Therefore, it seems that BRM and SYD are not completely functionally redundant and appear to control only a small subset of genes in common (Kwon et al. 2005, Bezhani et al. 2007). This phenotypic pleiotropy suggested that SNF2 chromatin-remodeling ATPases regulate the transcription of developmental genes (Peterson and Workman 2000). SYD is required for the up-regulation of *WUS* transcription in the shoot apical meristem (Kwon et al. 2005). The WUS homeodomain protein is expressed in the organizing center and signals overlying stem cells to maintain meristem homeostasis. *SYD* and *BRM* are redundantly required for the activation of *AP3* (B-class gene) and *AG* (C-class gene) in flower patterning via physical interaction with two direct transcriptional activators of class B- and C-class gene expression: LFY and SEP3 (Smaczniak et al. 2012, Wu et al. 2012). Homeotic conversion of floral organs and reduced expression of B-class genes are observed in the *brm* mutant, the *lfy-5 syd-1* double mutant and the *brm syd* double mutant. The *syd* mutant can partially

rescue the phenotype of the *clf* mutant, indicating that the function of the SWI/SNF ATPase might be similar to that of trxG proteins. SYD is also directly recruited to promoters to up-regulate positively the expression of selected genes downstream of the jasmonate and ethylene signaling pathways for resistance against biotic stress (Walley et al. 2008).

PICKLE

PKL, a member of the CHD3/4 family, contains a zinc finger homeodomain and two chromodomains arranged in tandem. It functions as an ATP-dependent chromatin-remodeling factor (Ho and Crabtree 2010). The *pkl* mutant exhibits spontaneous somatic embryogenesis with pickle-like, green, tuberous roots; reduced apical dominance; delayed flowering; anther dehiscence; and carpel polarity defects (Ogas 1997, Eshed et al. 1999, Henderson et al. 2004). In Arabidopsis, HDA6 and HDA19 may function together with PKL to remove acetylation marks (Li et al. 2005, Tanaka et al. 2008). PKL physically interacts with different types of transcription factors: PHYTOCHROME INTERACTING FACTOR 3 (PIF3) in light signaling, BRASSINAZOLE-RESISTANT 1 (BZR1) in BR signaling and SEP3 in floral organ identity control (Smaczniak et al. 2012, Zhang et al. 2014). In the root meristem, PKL functions antagonistically with PcG proteins to regulate meristematic growth, suggesting that H3K27me3 mark maintenance has an important role in fine-tuning the expression of meristematic genes (Hay et al. 2002, Aichinger et al. 2011). PKL may act indirectly by promoting the expression of PRC2 (Aichinger et al. 2009) or may bind directly to H3K27me3-enriched genes to affect acetylation levels (Zhang et al. 2012).

TOPLESS

The WD40 domain proteins TPL and TPL-related (TPR) interact directly and indirectly with transcription complexes involved in auxin and jasmonate signal transduction, meristem specification/maintenance and host defense (Szemenyei et al. 2008, Pauwels et al. 2010, Zhu et al. 2010). In the *tpl-1* dominant-negative mutant, loss of *TPL* causes up-regulation of the *AINTEGUMENTA*-like transcription factors *PLETHORA1/2* (*PLT1/2*), resulting in homeotic conversion of shoot tissue to root tissue at higher temperatures. This conversion occurs via antagonism of HD-ZIPIII transcription factors, which function to specify the apical fate (Smith and Long 2010). In the shoot apical meristem, WUS recruits TPL/TPR co-repressors to repress differentiation genes, hence ensuring stem cell specification (Kieffer et al. 2006). TPL/TPR further recruits HDAs to mediate histone deacetylation (Long et al. 2006), including type A Arabidopsis response regulator (ARR) genes, which are transcriptional targets of cytokinin signaling (D'Agostino et al. 2000, Leibfried et al. 2005). Several transcription factors, including *AP2* and *AGL15/18*, probably recruit *TPL* to repress *FT* transcription to regulate flowering time (Causier et al. 2012). *TPL* also plays an important role in floral organ specification. Recruitment of TPL/TPR by AP2 and LEU is necessary to define the boundary of whorls via spatial repression of the floral homeotic genes *AP3*, *PI* (B-class gene), *SEP3* (E-class gene) and *AG* (C-class gene) (Dinh et al. 2012, Krogan et al. 2012). In *tpl-1* and *tpl-1 ap2-2* −/+, both *AP3* expression and *SEP3* expression can be clearly detected in whorl 1 organs. By binding to the *AG* intron, *AP3* promoter and *SEP3* promoter, the AP2–TPL–HDA19 complex has been suggested to fine-tune *AG*, *AP3* and *SEP3* expression and restrict petal fate by maintaining the organ boundaries during organogenesis. In rice, ABERRANT SPIKELET AND PANICLE1 (ASP1) encodes a transcriptional co-repressor that is related to Arabidopsis TPL. The rice *asp1* mutant demonstrated pleiotropic phenotypes such as aberrant spikelet morphology, phyllotaxy disarrangement and dysfunction in auxin signaling (Yoshida et al. 2012).

Cross-Talk Between Chromatin Status and Gene Transcription

Unlike in animals, there are currently no known pioneer transcription factors in plants (Zaret and Carroll 2011). These transcription factors can bind to condensed chromatin and function to recruit chromatin-remodeling factors onto target genes for chromatin opening and transcription initiation. However, in Arabidopsis, the floral homeotic protein AG, which binds to the *KNU* promoter, triggers the progressive removal of H3K27me3 from the *KNU* locus, leading to subsequent transcriptional activation of *KNU* (Sun et al. 2014). It is known that AG binds to the CArG boxes located 1 kb upstream of *KNU*, and, coincidentally, that region harbors a PRE element, which is also bound by PcG protein. Through eviction of PcG from the *KNU* locus during stage 3 of flower development, the repressive H3K27me3 mark on the *KNU* TSS and gene body is progressively diluted through cell cycle progression. In this manner, *KNU* is induced at floral stage 6 for termination of floral stem cells. Another study also suggested that AG itself, from stage 3, may also recruit PcG for mild repression of *WUS* (Liu et al. 2011).

In other studies, several floral homeotic gene loci have been reported to be associated with the H3K27me3 demethylase REF6 (Lu et al. 2011). The *REF6* overexpression phenotype is similar to that of the *clf* and *tfl2* mutants, and the *ref6* mutant can partially rescue the curly leaf phenotype of *clf*. A recent study on the function of MADS-domain transcription factor complexes in Arabidopsis flower development suggested that AG protein complexes might contain REF6 (Smaczniak et al. 2012). This suggests that MADS-domain proteins may closely interact with chromatin-remodeling factors to facilitate chromatin opening and transcription initiation. Further evidence from the same study also indicates that SEP3 and REF6 are both included in a large complex, and PI may physically interact with chromatin remodelers of CHR4, CHR11 and CHR17, the ISWI-type nucleosome remodelers participating in genome-wide nucleosome distribution (Li et al. 2014). Furthermore, CHR4, CHR11 and CHR17 are also found in various complexes formed by AG, AP3, SEP3 and AP1 (Smaczniak et al. 2012). Possibly through interaction with REF6, AP1 is also suggested to be required for the removal of H3K27me3 from SEP3 in the very early stages of flower development.

In a very recent study on the dynamic regulation of chromatin accessibility by MADS-domain transcription factors in flower development, AP1 and SEP3 were suggested to bind their targets even before the target gene chromatins were fully open (Pajoro et al. 2014), suggesting that MADS-domain proteins may function as pioneer transcription factors. Furthermore, AP1 and SEP3 have been suggested to retain the ability to modulate the chromatin accessibility of their target genes, hence facilitating access to those genes by other transcription factors.

After the nucleosome structures open, the Mediator complex links transcriptional regulator binding at gene promoters with changes in the activation of RNA polymerase II (Conaway and Conaway 2011). The plant Mediator complex is estimated to be composed of >30 protein subunits (Mathur et al. 2011). Thus far, none of the Mediator subunit mutants has shown flower-specific defects; however, these subunits must play essential roles in transcriptional gene activation in flower development.

Summary and Future Perspectives

Studies of flower development over the last 30 years have revealed a large number of key regulatory genes and genetic networks. Floral organ identity and stem cell activity are regulated by the combinatorial action of floral homeotic proteins, which control different classes of transcription factors, hormone biosynthetic genes, signaling molecules and epigenetic regulators to control downstream events (**Fig. 2**). Studies have revealed that one homeotic protein can bind to thousands of target sites by forming higher order complexes. Homeotic proteins, transcription factors, hormones and epigenetic factors may converge and regulate the expression of multiple common downstream genes to perform complex developmental processes. These processes involve floral organ identity specification, floral organ formation and differentiation, and other important floral developmental programs including floral meristem maintenance and termination, floral organ patterning and boundary formation, and gametophytic development. During flower development the chromatin-remodeling factors appear to associate and bind to specific target genes to achieve spatiotemporal-specific expression in flower development. There are multiple balancing mechanisms that allow fine-tuning of gene expression in a single cell, and these mechanisms sometimes utilize antagonistic factors such as histone-modifying enzymes of the H3K27me3-depositing PcG complex, H3K27me3-removing JMJ histone demethylases, HATs and HDACs. However, several major questions remain, including (but not limited to) how each target is regulated in a temporal- and spatial-specific manner by particular complexes, how multimeric complexes are assembled at specific loci during flower development, how particular players co-ordinate the cross-talk between the intrinsic developmental program and extrinsic environmental cues, and how the robust and divergent effects of transcription factors, hormone signaling factors and chromatin factors are co-ordinated and converge to produce a robust genetic network for the formation of species-specific size, number and shape of floral organs downstream of the conserved ABC functions. Answering these questions in multiple model systems will allow us to understand fully the beauty of flower development.

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