Journal of Plant Physiology 214 (2017) 16–27

Contents lists available at ScienceDirect

Journal of Plant Physiology

journal homepage: www.elsevier.com/locate/jplph

Review article

Plant hormone signaling in flowering: An epigenetic point of view

Gerardo Campos-Rivero, Pedro Osorio-Montalvo, Rafael Sánchez-Borges, Rosa Us-Camas, Fátima Duarte-Aké, Clelia De-la-Peña*

Unidad de Biotecnología, Centro de Investigación Científica de Yucatán, Mexico

ARTICLE INFO

Keywords:
Auxins
DNA methylation
miRNAs
Histone modifications
Flowering
Phytohormone

ABSTRACT

Reproduction is one of the most important phases in an organism's lifecycle. In the case of angiosperm plants, flowering provides the major developmental transition from the vegetative to the reproductive stage, and requires genetic and epigenetic reprogramming to ensure the success of seed production. Flowering is regulated by a complex network of genes that integrate multiple environmental cues and endogenous signals so that flowering occurs at the right time; hormone regulation, signaling and homeostasis are very important in this process. Working alone or in combination, hormones are able to promote flowering by epigenetic regulation. Some plant hormones, such as gibberellins, jasmonic acid, abscisic acid and auxins, have important effects on chromatin compaction mediated by DNA methylation and histone posttranslational modifications, which hints at the role that epigenetic regulation may play in flowering through hormone action. miRNAs have been viewed as acting independently from DNA methylation and histone modification, ignoring their potential to interact with hormone signaling – including the signaling of auxins, gibberellins, ethylene, jasmonic acid, salicylic acid and others – to regulate flowering. Therefore, in this review we examine new findings about interactions between epigenetic mechanisms and key players in hormone signaling to coordinate flowering.

1. Introduction

Successful reproduction ensures a species' survival. All organisms – humans, animals, insects, plants, fungi – need to reproduce, either sexually or asexually. In the case of angiosperms, flowering is the major developmental transition from the vegetative to the reproductive stage, and requires genetic and epigenetic reprogramming throughout seed production (Amasino, 2010; Andrés and Coupland, 2012; Blümel et al., 2015). Internal and external factors such as day length (photoperiodism), temperature (vernalization), and hormones mediate the initiation of cell differentiation in the apical meristem in order to achieve each reproductive stage (Amasino, 2010; An et al., 2004; Burgarella et al., 2016; Kazan and Lyons, 2016; Reeves and Coupland, 2001; Sun et al., 2014).

In *Arabidopsis thaliana*, the transition from the vegetative to the reproductive stage is made by the suppression of leaf production and the establishment of a floral fate in the apical meristems (Koornneef et al., 1998). When the plant has passed from the juvenile to the adult phase and from the vegetative to the reproductive stage, the plant can be induced to flower. Flowering is regulated by an integrated network of several chemical and genetic pathways, where *CONSTANS* (*CO*) in the presence of light is a key regulator of flower promotion through the activation of *FLOWERING LOCUS T* (*FT*) and *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*) in long-day (LD) conditions (Putterill et al., 2004; Samach et al., 2000; Suarez-Lopez et al., 2001; Valverde et al., 2004). FT is a crucial mobile signal known as "florigen" that activates meristem identity genes and *SOC1*, which encodes to a MADS-box transcription factor, is present in the inflorescence meristem (Kardailsky et al., 1999; Kobayashi et al., 1999; Samachet al., 2000; Turck et al., 2008). *SOC1*, although it is activated by *CO,* can also be repressed by *FLOWERING LOCUS C* (*FLC),* a repressor of the floral transition (Michaels and Amasino, 1999, 2001; Mouradov et al., 2002). On the other hand, in short-day (SD) conditions, *Heading date* (*Hd*) *1* and *3a* encode genes similar to those found in the long-day pathway. *Hd1* encodes to an orthologue of *Arabidopsis CO*, while *Hd3a* is similar to *FT* (Kojima et al., 2002; Yano et al., 2000). The flowering time – the timing of the transition from vegetative to reproductive development – is affected by environmental conditions as well as hormonal action (Davies, 1995; Denay et al., 2017; Koornneef et al., 1998).

Different studies indicate the importance of the interactions among different plant hormones, such as ethylene (ET), indole-3-acetic acid (IAA), cytokinins (Cks) and abscisic acid (ABA) for flower induction in

* Corresponding author at: Unidad de Biotecnología, Centro de Investigación Científica de Yucatán, Calle 43 No. 130 x 32 y 34, Col. Chuburná de Hidalgo, 97205 Mérida, Yucatán, Mexico.

E-mail addresses: ingcampos43@gmail.com (G. Campos-Rivero), pedro.osorio@cicy.mx (P. Osorio-Montalvo), rcsb88@gmail.com (R. Sánchez-Borges), rosa.us@cicy.mx (R. Us-Camas), fatima.duarte@cicy.mx (F. Duarte-Aké), clelia@cicy.mx (C. De-la-Peña).

http://dx.doi.org/10.1016/j.jplph.2017.03.018
Received 10 October 2016; Received in revised form 6 March 2017; Accepted 29 March 2017
Available online 31 March 2017
0176-1617/

A. thaliana (Domagalska et al., 2010; Matsoukas, 2014), apples (Sanyal and Bangerth, 1998) and *Pharbitis nil* (Frankowski et al., 2014; Kęsy et al., 2008). It is also known that hormonal signaling has an important role in flowering through the regulation of *FLC*, *CO* and *FT*. For instance, salicylic acid (SA) is involved in the regulation of the transcription of *CO, FLC, FT* and *SOC1* (Martínez et al., 2004). Intriguing discoveries have shown that the late flowering phenotype of SA-deficient plants correlates with a 2–3-fold expression of *FLC*, decreasing the levels of *FT* compared with wild-type plants in LD or SD conditions. Furthermore, the dynamic change in the expression of these genes involves chromatin modifications (Berr et al., 2015; Blümel et al., 2015, Hepworth and Dean, 2015; Kang et al., 2015; Picó et al., 2015; Sun et al., 2014). For instance, the expression of *FLC* and *FT* in *Arabidopsis* are epigenetically regulated (Hepworth and Dean, 2015; Ietswaart et al., 2012; Swiezewski et al., 2009). Some reports highlight the function of the Polycom Repressive Complex 2 (PRC2) in the silencing of the floral repressor *FLC* locus by the histone mark H3K27me3 during a prolonged period of cold (Buzas et al., 2011; De Lucia et al., 2008; Yuan et al., 2016), while others claim that the regulation of *FLC* is accomplished by the reduction of H3K4me2 levels in this gene (Liu et al., 2010; Liu et al., 2007a). In fact, both regulatory histone marks are involved in the regulation of *FLC* by a coordinated association of the PRC2 and Flowering Locus D (FLD) complexes (Shafiq et al., 2016). *FLD* gene encodes a histone demethylase that mediates the enzymatic demethylation of H3K4me2 and facilitates deacetylation of histone H4 in *FLC* chromatin (Liu et al., 2007a), although Jin et al. (2008) found that the sumoylation/desumoylation activity of FLD could control histone acetylation/deacetylation by an unknown mechanism.

2. Epigenetic modifications and plant hormone regulation in flowering

Covalent modification of cytosine residues by DNA methyltransferase enzymes allows the incorporation of a methyl group at the 5′ position of the pyrimidine ring of the cytosines in order to establish the DNA methylation state of the chromatin (Allis et al., 2015; Bird, 1986; De-la-Peña et al., 2015). Histone modifications − phosphorylation, acetylation, methylation, ubiquitination, etc. − also work on chromatin compaction by "writers" and "erasers" that can modify the histone tails of the nucleosome (Allis et al., 2015). On the other hand, miRNAs, which are small, endogenous and non-translated single-strand RNA (21–24 nucleotides), can regulate gene expression by guiding the cleavage of complementary mRNA targets (Bartel, 2004; Jones-Rhoades et al., 2006). Epigenetic mechanisms, which regulate transcription acting on chromatin conformation that are determined by DNA methylation, histone posttranslational modifications and chromatin remodeling, have been documented in flowering (Jeong et al., 2015; Liu et al., 2016; Teotia and Tang, 2015) and hormone regulation (Yamamuro et al., 2016). Also, a recent review examined the participation of miRNAs during these processes (Hong and Jackson, 2015; Liu et al., 2009). Therefore, for this review, we chose to focus on how DNA methylation, histone modifications and miRNAs cooperate with plant hormone signaling to coordinate flowering in higher plants.

2.1. Auxins

The plant hormone auxin is necessary for normal plant growth and development, as it regulates a variety of developmental processes such as cell elongation and division, organ patterning, root and shoot development and tropic responses to light and gravity (Dinesh et al., 2016; Kasahara, 2015). In higher plants, the main natural auxin is indole-3-acetic acid (IAA), which is synthesized in young leaves, cotyledons, expanding leaves and root tissues (Ljung et al., 2001); however, indole-3-butyric acid (IBA) and 4-chloroindole-3-acetic acid (4-Cl-IAA) are also natural auxins. The synthetic auxins naphthalene-1-acetic acid (NAA) and 2,4-dichlorophenoxyacetic acid (2,4-D) are metabolically more stable and commercially available and are highly used in plant *in vitro* culture techniques. Nevertheless, they do not share their mechanism of action with native IAA (Simon and Petrásek, 2011), and the concentrations used for *in vitro* purposes could have different outcomes (Us-Camas et al., 2014).

The exposure to different concentrations of synthetic auxins causes epigenetic changes that affect the normal development of flowers (Jaligot et al., 2000). For instance, the mantled phenotype of the African oil palm (*Elaeis guineensis* Jacq.), which is characterized by abnormalities in its floral development, can result in altered sensitivity and/or response to the auxins/cytokinin ratio (Eeuwens et al., 2002; Jaligot et al., 2011). The appearance of mantled flowers was found to increase when high concentrations of kinetin (0.25 mg l^{-1}) and low concentrations of the synthetic auxin NAA (0 or 0.1 mg l^{-1}) were used. On the contrary, when high levels of NAA (0.5 mg l^{-1}) were used, a reduced incidence of mantled flowers was observed (Eeuwens et al., 2002). It has been suggested that kinetin induces DNA hypomethylation, generating the mantled phenotype, while NAA causes DNA hypermethylation, resulting in the opposite phenotypic effect (Eeuwens et al., 2002; Jaligot et al., 2011; Jaligot et al., 2000). There is a positive correlation between a reduction in global DNA methylation (from 5% to 2.5%) and the appearance of the mantle phenotype (Jaligot et al., 2000).

A strict control of auxin homeostasis and the maintenance of an appropriate level of IAA is important for normal growth and development (Davies, 2010). IAA is transported to the growing regions and, normally, high IAA content correlates with intense cell division (Ljung et al., 2001; Tanaka et al., 2006). The polar movement of IAA allows a differential distribution or gradient of auxin within the plant tissues, and these changes are dynamic during developmental processes such as flowering (Cheng and Zhao, 2007; Tanaka et al., 2006). PIN-FORMED (PIN) proteins are important components of auxin efflux and their subcellular localization guides the flow of auxins (Tanaka et al., 2006). In *Arabidopsis*, the *pin-formed mutant pinl-1*, which disrupts the normal polar transport of auxins, fails to form the floral primordia and presents a pin-shaped inflorescence devoid of flowers (Okada et al., 1991). This condition can be reversed when IAA is applied exogenously, inducing floral formation (Reinhardt et al., 2000). The *met1-6* mutants also present defects in the establishment of an auxin gradient, a highly perturbed *PIN1* promoter activity, and a late-flowering phenotype (Xiao et al., 2006). Floral primordium initiation not only requires a local maximum of auxin but also the activity of AUXIN RESPONSE FACTOR MONOPTEROS (MP/ARF5) (Przemeck et al., 1996; Yamaguchi et al., 2013) and, like *PIN1* mutants (Okada et al., 1991), *MP* mutants form naked inflorescence stalks lacking flowers (Przemeck et al., 1996). MP targets are key regulators of floral growth initiation such as LFY, AINTEGUMENTA (ANT) and AINTEGUMENTA-LIKE 6 (AIL6) (Elliott et al., 1996; Krizek and Eaddy, 2012; Schultz and Haughn, 1991; Wu et al., 2015; Yamaguchi et al., 2013). Wu et al. (2015) suggest that under high levels of auxin, MP recruits SWI/SNF proteins, implicated in transcriptional control via chromatin remodeling, to regions of chromatin that contain genes involved in flower formation. This changes the chromatin state that enables the transcriptional activation of genes promoting the initiation of flower primordium (Wu et al., 2015).

The involvement of histone modifications in the transcriptional regulation of auxin target genes has also been documented (Wu et al., 2015). It has been reported that auxin treatments lead to an increase of H3K9ac in *LFY* and *FILAMENTOUS FLOWER (FIL)* loci, which causes an increase in mRNA accumulation of both genes, promoting floral primordium initiation (Wu et al., 2015). On the other hand, only in the absence of auxin application do the transcriptional co-repressor TOPLESS (TPL) and HDA19 occupy the MP-bound sites at the *LFY* and *FIL* in the inflorescence apices, preventing transcription of these genes (Wu et al., 2015). SWI/SNF ATPases subgroup BRAHMA (BRM) and SPLAYED (SYD) activities increase in accessibility at the MP target for flower primordium initiation. Plants generated using *syd-5* mutants