Evolution of the Flowering Pathways

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Contents

1 Introduction
2 The Evolution of the Photoperiod Pathway
  2.1 Photoperiod Pathway in Vascular Plants
  2.2 Compared Evolution of Photoperiodic Signaling in Green Algae and Land Plant
3 Overcoming Temperature Changes
  3.1 Vernalization
  3.2 Ambient Temperature
4 Nutrients Signaling to Flowering
5 Flower Development
  5.1 Floral Identity Determination
  5.2 Floral Organ Identity Determination
6 Conclusions
References

Abstract Flowering plants are some of the most successful organisms on Earth, particularly those used in agriculture due to the widespread distribution produced by farming activities. The correct moment of the year to flower is a crucial decision as it strongly compromises the success of the progeny and is thus strictly controlled. Crops have been artificially selected to flower in those conditions better adapted for human production, and many genes related to flowering time are selected as targets for breeding programs. These characteristics reflect a complex regulatory pathway

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that has to respond both to predictable and unexpected changes in the environment. This plasticity confers the flowering plants with a genetic toolkit to adapt to varied habitats and changing environmental conditions. Recent advances in massive acquisition of data from many different species belonging to the green eukaryotic lineage allow us to make an evolutionary approach to the main mechanisms that influence the floral transition and how flowers are formed in modern plants. This work will review some of these aspects from the floral transition to the floral organogenesis.

1 Introduction

The flowering transition is one of the most important developmental decisions that a plant has to take during its life cycle. An incorrect decision to flower has a strong negative influence on the capacity of the plant to transmit its genes to the next generation, and thus it is strictly regulated (Casal et al. 2004). This decision is strongly influenced by external and internal cues among which light, temperature and nutrient signals are probably the most influential (Amasino 2010). In order to understand the complex signaling events that promote or inhibit flowering, different pathways have been proposed and excellent reviews have been recently published (Smeekens et al. 2010; Huijser and Schmid 2011; Andrés and Coupland 2012; Song et al. 2012a, b, c), but they can all be directly or indirectly grouped into three groups (Fig. 1). The light pathway integrates those signals derived from the light quality, day length, or the circadian clock. The internal signals comprise those provided by hormones, nutrients (sugar, nitrogen compounds, etc.) and age. The temperature signals include the so-called autonomous pathway, the ambient temperature signals and the vernalization signals. These pathways will be described in more detail below.

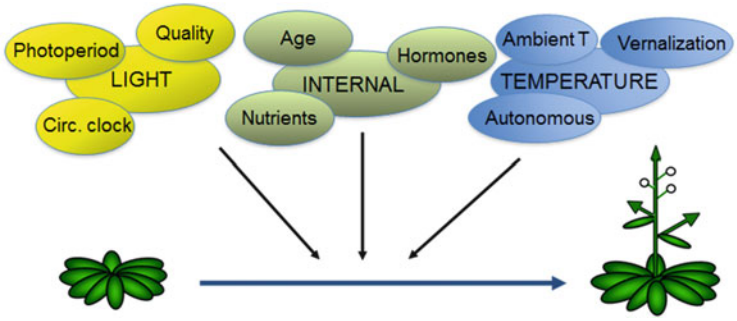

Fig. 1 Major pathways controlling the floral transition in *Arabidopsis*. Schematic representation of the three major cues that influence the floral transition in *Arabidopsis*. Light (*yellow*) includes photoperiodic, light quality, and circadian clock. Temperature (*blue*) includes vernalization, autonomous and ambient temperature signals. Internal (*green*) includes the effect of hormones, age, sugars and other metabolites (nutrients)

Most of the plants will flower when one, or a combination of these signals, reaches the threshold that triggers the floral transition. This is coordinated by a network of genes that is highly conserved throughout evolution (Romero-Campero et al. 2013). In this work we will review recent knowledge about the gene networks that control the flowering pathways as well as floral organogenesis and how can we trace back this gene toolkit into the evolutionary story of plants. It will allow us to understand the origin of the flowering pathways and why they have reached such complexity in angiosperms. Inevitably, *Arabidopsis thaliana* will be the model to follow, as most of the flowering work has been done in this small brassica. Nevertheless, we will try to extrapolate this information into other plants representing different phylogenetic relationships and evolutionary steps within the green eukaryote lineage.

We will also review the process of floral organogenesis because it is chronologically and locally connected to the last stages of the floral transition within the shoot apical meristem (SAM). In this way, many of the late genes involved in the floral transition, including the floral integrators, control the early stages of floral formation. This assures the continuity in the signaling process necessary to achieve the successful step-by-step hierarchy of floral organogenesis.

2 The Evolution of the Photoperiod Pathway

The amount of incident light at a particular point on most of the Earth's surface changes throughout the year resulting in the different seasons, particularly in the middle half of the hemispheres where most of the human population is concentrated. Animals and plants have developed throughout their evolution molecular tools consisting in genes and signaling networks that transduce day length information (or photoperiod) into the regulation of key developmental and metabolic processes. This capacity is known as photoperiod response (Bradshaw and Holzapfel 2007).

2.1 Photoperiod Pathway in Vascular Plants

One of the most conserved day length responses among plants is the photoperiodic flowering pathway (Romero-Campero et al. 2013). *CONSTANS* (*CO*) is the central gene in this pathway and promotes flowering by inducing the expression of the florigen *FLOWERING LOCUS T* (*FT*) gene (Valverde 2011). Recent advances in genomics of vascular plants have allowed researchers to identify several genes that control flowering in species such as potato (Martínez-García et al. 2002), tomato (Corrales et al. 2014), sorghum (Murphy et al. 2011), rice (Yano et al. 2000) and *Jatropha* (Yang et al. 2011). Nevertheless, the long-day (LD) facultative plant

Arabidopsis thaliana is the model organism where most studies have been performed (Amasino 2010).

In *Arabidopsis*, *CO* and *FT* expression are regulated by circadian and photoperiodic regulatory elements. In this sense, CYCLING DOF FACTOR (CDF) proteins are a group of four DOF transcription factors that bind to the *CO* and *FT* promoters negatively regulating their expression (Imaizumi et al. 2005; Fornara et al. 2009; Song et al. 2012c). At the end of a LD, the blue light-dependent GI-FKF1 complex induces CDF degradation (Rubio and Deng 2007), allowing FLOWERING BHLHs (FBHs) to enhance *CO* expression (Ito et al. 2012) and thereby *FT* induction. Moreover, GIGANTEA (GI) is involved in *FT* induction in a CO-independent way (Sawa and Kay 2011; Srikanth and Schmid 2011). *CO* expression is also regulated at the transcriptional level by the circadian clock whose core is constituted in *Arabidopsis* by the genes *CIRCADIAN CLOCK ASSOCIATED 1* (*CCA1*), *LATE ELONGATED HYPOCOTYL* (*LHY*), and *TIMING OF CAB EXPRESSION 1* (*TOC1*) (McClung 2014). Additionally, *CO* is posttranslationally regulated by the 26S proteasome due to the action of two E3 ubiquitin ligases with Ring Finger domains: CONSTITUTIVE MORPHOGENIC 1 (COP1) during the night and HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 1 (HOS1) during the morning (Jang et al. 2008; Lazaro et al. 2012). Moreover, light has an important role in the regulation of *CO* expression. The photoreceptor PHYTOCHROME B (PHYB) promotes CO degradation by red light, whereas CRYPTOCHROMES 1 and 2 (CRY1, CRY2) and PHYTOCHROME A (PHYA) promote its stability through a blue light signal (Valverde et al. 2004) specifically during the daylight period. This complex regulatory network determines that *CO* mRNA coincides with a high stable protein level during the evening of a LD (external coincidence model) (Andrés and Coupland 2012) triggering the expression of the florigen *FT* gene. However, depending on its geographical location, plants have developed different regulatory mechanisms to anticipate photoperiod changes. For example, in short-day (SD) plants, such as rice (*Oryza sativa*), an *FT* homolog (*HEADING DATE 3a, HD3A*) is induced in SD by a CO homolog (HD1), whereas in LD HD1 behaves as a repressor of *HD3A* (Turck et al. 2008). Additionally, transgenic rice overexpressing *CDF* homologs (*OsDOF12*) induces *HD3A* expression only under LD conditions in a *HD1*-independent manner (Li et al. 2009). In this species, GI promotes *HD1* expression although it is yet unknown whether this regulation is direct or through a FKF1/CDF route similar to the one in *Arabidopsis* (Higgins et al. 2010).

The regulatory differences observed in vascular plants may reflect an evolutionary divergence produced by the needs to adapt to specific environmental conditions. This could explain the emergence of new regulatory genes involved in the same processes or the change in function of a specific gene. For example, in rice EARLY HEADING DATE 1 (EHD1), a B-type response regulator, induces *HD3A* transcription in SD conditions, independently of HD1 (Doi et al. 2004) and the GRAIN NUMBER, PLANT HEIGHT, and HEADING DATE 7 (GHD7) rice protein plays a key role in the photoperiod pathway (Xue et al. 2008). Nevertheless, no putative *Arabidopsis* orthologs of these genes have been identified so far. In potato, similar

genes to those that control the floral transition also regulate other biological pathways such as tuberization. Both processes are finally controlled by two different *FT*-like paralogues, *StSP3D* that promotes flowering and *StSP6A* that regulates tuber formation (Navarro et al. 2011) in two separated transduction pathways. *StSP3D* and *StSP6A* respond to different photoperiod conditions involving the StGI-StFKF1 complex, StCDF, and StCO protein (Kloosterman et al. 2013). Interestingly, in neutral-day plants, where flowering time is not controlled by photoperiod, CDFs are involved in other biological processes not related to the photoperiod response. For example, in tomato, *SlCDFs* are induced in response to abiotic stress conditions. Nevertheless, the *SlCDF* heterologous expression in *Arabidopsis* delays flowering by reducing *CO* and *FT* transcript levels. This suggests that the ability of SICDFs to control the photoperiod response is conserved although it is not involved in the floral transition in these plants (Corrales et al. 2014).

Strikingly, flowering gene regulatory networks from a wide range of photosynthetic organisms share a large set of orthologs. This suggests that the photoperiodic gene regulatory network evolved very early in the green evolutionary linage constituting an ancestral network. The current photosynthetic organisms have then inherited this gene network from these common ancestors.

2.2 *Compared Evolution of Photoperiodic Signaling in Green Algae and Land Plants*

The latest results from our group and others (Serrano et al. 2009; Romero-Campero et al. 2013) have demonstrated an exclusive origin of the photoperiod response in algae of the Chlorophyceae class, which would have then evolved into the complex pathway of modern plants. In this section we will try to dissect the evolutionary processes involved.

2.2.1 Homolog Genes in *Chlamydomonas*

CONSTANS Homolog

Chlamydomonas reinhardtii is considered to be a living representative of the common ancestor that gave rise to the green eukaryotic lineage. The first gene related to the photoperiod pathway identified in the *Chlamydomonas* genome was a single-copy *CO* homolog, called *CrCO* (Serrano et al. 2009; Valverde 2011). *CrCO* was shown to be involved, among other mechanisms, in processes controlled by the circadian clock, such as starch synthesis and cell growth. Surprisingly, transgenic plants overexpressing *CrCO* under a constitutive or phloem-specific promoter, flowered earlier than WT and in a similar way to plants overexpressing the original *CO* gene. *CrCO* can, thus, complement *co* mutation. In contrast, *CO like 1* (*COL1*)

is unable to complement *co* mutation in spite of being evolutionarily more related to *CO* than *CrCO*. Possibly, CO and CrCO share key structural similarities that are not reflected in the alignment of their sequences, which shows very low general amino acid identity. This constitutes an example of the limitations of using solely sequence similarity when detecting potential orthologs (Romero-Campero et al. 2013). Recently, evidence of the high relevance of the *CrCO* gene in the algae transcriptome has been suggested by gene co-expression analysis. It has been shown that the *CrCO* gene constitute a hub gene in a gene co-expression network constructed based on RNA-seq data from a wide range of relevant physiological conditions (Romero-Campero et al. 2013). A single-copy *CrCO* gene has evolved into numerous *CONSTANS-LIKE* (*COLs*) gene families in *Physcomitrella* (*PpCOLs*) and *Arabidopsis* (*AtCOLs*), establishing complex and robust networks with greater numbers of hub genes in both species (Romero-Campero et al. 2013). This diversification of the *COL* family in *Physcomitrella* and vascular plants and the high overlapping between their functions indicate that the different biological processes in which CrCO, PpCOLs, and AtCOLs are involved are highly conserved across evolution (Romero-Campero et al. 2013). Additionally, COLs may have a wide repertoire of plant-specific light-dependent functions besides those already described (Valverde 2011) such as axillary ramification (Wang et al. 2013), bud dormancy (Böhlenius et al. 2006), and tuber growth (González-Schain et al. 2012).

CDF Homologs

The genome of *Chlamydomonas* contains another single-copy gene called *CrDOF* that seems to be part of the ancestral photoperiod pathway. *CrDOF* evolution has produced a numerous gene family, the DOF transcription factors (TFs), following a similar evolutionary history as *CrCO*. DOFs are specific TFs in vascular plants (Moreno-Risueño et al. 2007) and are not present in animal or fungi genomes. Specifically, *Arabidopsis* has 36 DOF proteins (Noguero et al. 2013) including the small family of four CDFs (Imaizumi et al. 2005; Fornara et al. 2009). In *Chlamydomonas*, CrDOF is regulated, in a similar way as CDFs in *Arabidopsis*, by the circadian clock and photoperiodic mechanisms. Additionally, like the CDFs, CrDOF controls *CrCO* transcription. Nevertheless, in contrast to the CDF function in *Arabidopsis*, CrDOF activates *CrCO* expression in *Chlamydomonas* by binding to its promoter. In addition, CrDOF controls important physiological processes in the algae exhibiting a surprisingly dual function, repressor or activator, depending on the day length. In this way CrDOF is able to induce cellular division by activating CrCO in SD, whereas in LD CrDOF represses the cell cycle progression to mitosis in a CrCO-independent manner. CrDOF phenocopies CDF function in *Arabidopsis* so that transgenic plants expressing *CrDOF* under different tissue-specific promoters delay flowering by suppressing *CO* and *FT* expression. Finally, RNA-seq data analysis revealed an apparent functional overlap between CrDOF and DOF proteins. These results reflect again how the functions of proteins involved in photoperiodic responses are extremely conserved across evolution.

The diversification and subsequent acquisition of new regulatory domains by CrDOF (which has only a DOF domain and nuclear localization signal) to vascular plant DOF factors could explain the new regulatory processes in which CDFs and other DOF proteins are involved (Lucas-Reina et al. 2015).

2.2.2 Putative Homologs

Several putative *Chlamydomonas* orthologs of *Arabidopsis* genes involved in the photoperiod response have been identified using non-curated bioinformatic methods such as the BBH (bidirectional best hit) method (Table 1). Their involvement in the photoperiod response in *Chlamydomonas* and their interactions with *CrCO* and *CrDOF* are yet to be validated experimentally. Here we analyzed the conservation of the co-expression patterns among these genes by comparing them to the co-expression patterns of homologs from *Arabidopsis* (Fig. 2).

Circadian Clock Genes

Approximately 30 putative genes have been identified in *Chlamydomonas* that are involved in the control of circadian processes. These genes are called *RHYTHM OF CHLOROPLAST* (*ROC*). Some of the codified proteins are specific from algae; others present conserved domains with plant circadian clock proteins (Matsuo and Ishiura 2011). Strikingly, other ROCs present domains similar to those found only in animal proteins involved in circadian rhythm control (Schulze et al. 2010). Specifically, ROC40 has a MYB domain similar to CCA1 and LHY proteins and ROC66, which presents B-box and CCT domains similar to CO, to COL1, involved in circadian clock (Ledger et al. 2001) and COL9 (Matsuo and Ishiura 2011). ROC66 CCT domain is also similar to the CCT domain from *Arabidopsis* TOC1 (Matsuo and Ishiura 2011). Besides the sequence similarity that *ROC40* and *ROC66* show with *CCA1*/*LHY* and *TOC1*, these two *Chlamydomonas* genes also exhibit similar co-expression patterns as their putative *Arabidopsis* orthologs. *CCA1*/*LHY* and *TOC1* present a negative co-expression pattern in *Arabidopsis*, which seems to be conserved in *Chlamydomonas*, as *CrLHY* and *CrTOC1* show a negative co-expression pattern (Fig. 2).

The conservation of the circadian clock core genes, *CCA1*/*LHY* and *TOC1*, has also been found in the green algae *Ostreococcus tauri*, although in this case, their expression patterns differ from those in the *Arabidopsis* genes (Bouget et al. 2014).

Photoreceptors

Light perception in plants is carried out by a set of different photoreceptors. One of them is the phototropin (PHOT) involved in physiological processes like phototropism and stomatal opening. On the other hand, cryptochromes (CRYs) and

Table 1 Genes involved in the photoperiod response in *Arabidopsis* and *Chlamydomonas*

Gene name	*Arabidopsis thaliana*	*Chlamydomonas reinhardtii*
CO	At5g15840	g6302
COL1	At5g15850	g6302
FT	At1g65480	Not identified
CDF1	At5g62430	Cre12.g521150
CDF3	At3g47500	Cre12.g521150
FBH1	At1g35460	Cre14.g620850
FBH4	At2g42280	Cre14.g620850
ZTL	At5g57360	Cre12.g518800
FKF1	At1g68050	Cre12.g518800
GI	At1g22770	Not identified
TOC1	At5g61380	g16738
LHY	At1g01060	Cre06.g275350
CCA1	At2g46830	Cre06.g275350
CRY1	At4g08920	Cre06.g295200
CRY2	At1g04400	Not identified
HOS1	At2g39810	g16152
COP1	At2g32950	Cre02.g098100

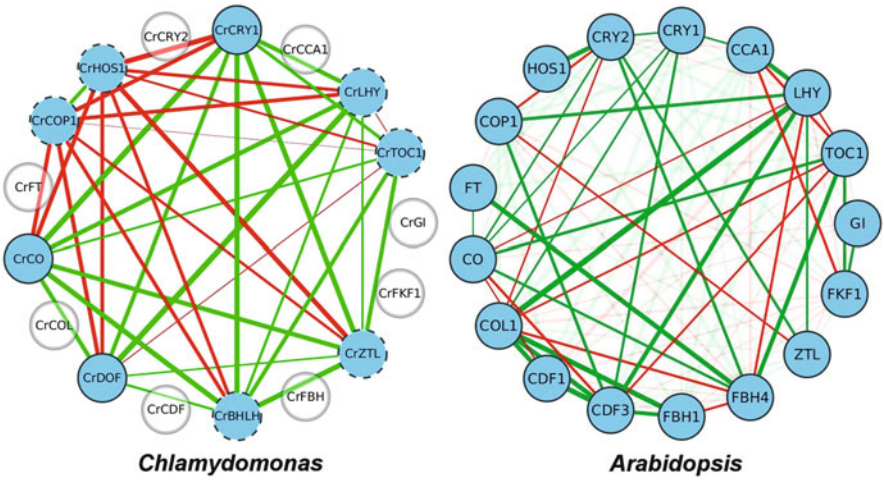

Fig. 2 Co-expression patterns between genes involved in the photoperiod response in *Chlamydomonas* and *Arabidopsis*. The figure represents co-expression relationships (*green*, positive; *red*, negative) between the genes (*blue circles*) involved in the photoperiod response in *Chlamydomonas* and *Arabidopsis*. A conserved co-expression pattern is apparent together with processes of gene duplication as well as specific network rewiring: the circadian clock genes *CCA1*/*LHY* and *TOC1* are negatively co-expressed in both organisms. Processes of gene duplication have produced *Arabidopsis* genes such as *CDF1* and *CDF3* from the *CrDOF*, or *CO* and *COL1* from *CrCO*, from *Chlamydomonas*. Nevertheless, while the positive co-expression between *CrDOF* and *CrCO* in *Chlamydomonas* has been conserved in the *Arabidopsis CDF1* and *COL1*, the co-expression between *CDF1* and *CO* is negative in *Arabidopsis*

phytochromes (PHYs) are involved in morphogenetic, photoperiodic, and circadian mechanisms like flowering.

PHOTs are the principal sensory molecules for light-dependent life cycle control in *Chlamydomonas* and other green algae like *Ostreococcus tauri*. PHOT is a modular protein formed by a light, oxygen, or voltage (LOV) domain, similar to that of the protein family ZTL-FKF1-LKP2, in the amino terminal part of the protein, followed by a carboxy-terminal histidine kinase (HK) domain (LOV-HK). In contrast to PHOTs that are specific of the green linage, the LOV-HK domain is related to the large family of LOV-HK domains found in different kinds of prokaryotes (Djouani-Tahri et al. 2011).

Chlamydomonas PHOTOLIASE HOMOLOG 1 (*CPH1*) encodes a protein with a significant sequence similarity with two plant-specific CRYs (CRY1 and CRY2) involved in the photoperiodic pathway. CPH1 levels are controlled by blue and red light, which induce the instability of the protein (Reisdorph and Small 2004). In this text we refer to *CPH1* as *CrCRY1*. Specific co-expression patterns such as the positive co-expression between *CrCRY1* and *CrCO* seem to be conserved in *Arabidopsis* between the genes *CRY1* and *CO*.

Moreover, in *Chlamydomonas* aCRY (animallike CRY) and DASH-CRYs (*Drosophila*, *Arabidopsis*, *Synechocystis*, and *Homo*-like CRY) (Beel et al. 2013) have been described, indicating that the evolutionary origin of cryptochromes precedes the green eukaryote lineage separation.

PHY-related proteins are a conserved multidomain protein found in bacteria (including cyanobacteria), fungi, and many eukaryotic algae like prasinophytes (green algae), heterokonts (diatoms and brown algae), and glaucophytes. All PHYs use bilin chromophores to sense light. Nevertheless, in algae unlike plants, PHY can sense orange, green, and blue light. In *Chlamydomonas*, in spite of retaining the ability to synthesize bilin, no protein with a significant sequence similarity with any PHY has been identified (Rockwell et al. 2014).

Flowering bHLH Homologs

FBH proteins are part of the large family of eukaryotic basic helix–loop–helix (bHLH)-type transcription factors. bHLHs present a wide diversity and a great number of genes in plant and mosses; in contrast, there is a small family in green and red algae. Particularly, in the *Chlamydomonas* genome only four bHLH genes have been identified (Riaño-Pachón et al. 2008; Carretero-Paulet et al. 2010; Pires and Dolan 2010). Only one of these genes presents significant similarity with bHLH genes present in higher plants such as *Arabidopsis*. We will refer to this gene as *CrbHLH*. The rest of *bHLH* genes seem to be specific of the Chlorophyceae. Additionally, *CrbHLH* exhibits positive co-expression patterns with genes such as *CrCO* and *CrCRY1*. These patterns are conserved in *Arabidopsis* between the genes *FBH4*, *CO*, and *CRY2*.

Constitutive Photomorphogenic 1 and High Expression of Osmotically Responsive Genes 1

COP1 and HOS1 are members of the E3 ubiquitin ligase family with a Ring-finger domain. Up to now, COP1 has been identified in plants and red algae like *Cyanidioschyzon merolae*, whereas HOS1 has been found only in plants (Riaño-Pachón et al. 2008). Nevertheless, recent updates of the web portal for plant comparative genomics Phytozome include potential *Chlamydomonas* orthologs for both genes. These genes have been identified using automatic bioinformatic tools such as the bidirectional best hit method. The conservation of certain co-expression patterns involving these genes supports their consideration as potential orthologs.

2.2.3 Unidentified Genes in Algae

Up to now, no *GI* and *FT* homologs have been identified in any alga species (Corellou et al. 2009; Piñeiro and Jarillo 2013). Therefore, these proteins may have been acquired later in evolution. In fact, the first evidence of a GI binding site in a DOF protein has been found in *Physcomitrella patens* (Lucas-Reina et al. 2015).

3 Overcoming Temperature Changes

Temperature is a key environmental variable that exerts a strong influence on the floral transition. Plants adapted to temperate climates are exposed to annual cold cycles but also to fluctuations of temperature within the different seasons; consequently, they need to differentiate the timing and interval of cold to bloom at the right time in order to increase their reproductive success (Preston and Sandve 2013). Many species from temperate climates require a prolonged exposure to cold in order to become competent to flower (Chouard 1960); this period is known as vernalization. The requirement for vernalization delays reproductive growth during winter minimizing the risk of frost damage to cold-sensitive reproductive organs and ensures that reproductive development and seed production occur in spring and summer (Amasino 2004, 2010; Kim et al. 2009). In addition, most plants in temperate regions face fluctuations in temperatures within the ambient range (above 10 °C) and should be able to perceive and integrate these signals (Samach and Wigge 2005). These non-stressful temperatures have been shown to strongly influence flowering time, causing either a delay or an acceleration of flowering (Westerman and Lawrence 1970; Blazquez et al. 2003). Interestingly, recent reports indicate that the ambient temperature changes are sensed and transduced differently than extreme temperature changes. Here, we will discuss the current knowledge at the molecular level on the mechanisms that control flowering

time in response to cold and non-stressful temperatures in different plant species, which will help us to understand the evolution of alternative mechanisms.

3.1 Vernalization

Vernalization responsiveness has evolved independently on multiple occasions (Greenup et al. 2011; Oliver et al. 2013); accordingly, genes controlling vernalization have been identified in different plant lineages (Danyluk et al. 1998; Michaels and Amasino 1999; Sheldon et al. 1999; Izawa et al. 2003; Trevaskis et al. 2003; Pin et al. 2010).

In *A. thaliana*, two genes, *FRIGIDA* (*FRI*) and *FLOWERING LOCUS C* (*FLC*), are the major natural determinants for the vernalization response (Shindo et al. 2005; Lovell et al. 2013; Li et al. 2014). The role of the single-copy gene *FRI* is to activate the expression of *FLC*, which is a MADS-box-type repressor that prevents flowering. Downregulation of *FLC* expression requires a long exposure to cold (Michaels and Amasino 1999). FRI induces *FLC* expression through direct interaction with the nuclear cap-binding complex (Geraldo et al. 2009; Crevillen and Dean 2011). In addition, recent studies have demonstrated that FRI-mediated upregulation of *FLC* is associated with epigenetic modifications, primarily to a marked increase in the histone H3 lysine 4 trimethylation (H3K4me3) pattern (Bastow et al. 2004; Sung and Amasino 2004a; Finnegan and Dennis 2007). The repression of *FLC* by cold involves different mechanisms (Song et al. 2012a). Briefly, an antisense transcript called *COOLAIR* is upregulated after 2–3 weeks of cold leading to the downregulation of *FLC* transcription (Swiezewski et al. 2009). In addition, a sense noncoding RNA (ncRNA) transcript, called *COLDAIR* (Heo and Sung 2011), is also induced by cold but later than *COOLAIR*. *COLDAIR* recruits the polycomb group complex VRN-PRC2 to *FLC* chromatin to mediate gene silencing through the incorporation of histone 3 lysine 27 trimethyl (H3K27me3) marks (De Lucia et al. 2008; Heo and Sung 2011; Crevillen et al. 2013; Kim and Sung 2014). Components of VRN-PRC2 complex are the VEFS domain containing protein VERNALIZATION 2 (VRN2), the SET-domain catalytic subunit CURLY LEAF (CLF) or SWINGER (SWN), FERTILIZATION-INDEPENDENT ENDOSPERM (FIE), and MULTICOPY SUPRESSOR OF IRA1 (MSI1) (Kim and Sung 2014). Additional components of the VRN-PRC2-mediated repression are the plant-specific B3 DNA-binding protein VRN1, and the plant homeodomain (PHD) motif containing proteins VERNALIZATION INSENSITIVE 3 (VIN3), VIN3-LIKE 1 (VIL1), and VERNALIZATION 5 (VRN5), which are nonredundantly necessary for the repression (Levy et al. 2002; Sung and Amasino 2004b; Sung et al. 2006; Greb et al. 2007). *VRN1*, *VRN2*, and *VIL1*/*VRN5* are constitutively expressed regardless of vernalization. In contrast, *VIN3* is only induced when plants are kept under prolonged periods of cold temperature and quickly decreases when plants are returned to warm growth temperatures. Therefore, *VIN3* is a cold-specific component of the vernalization pathway in *A. thaliana*

Table 2 *Arabidopsis* vernalization orthologs in monocots and brassicas

Arabidopsis thaliana	*T. aestivum H. vulgare*	*Brassica oleracea*	*Beta vulgaris*	*Arabis alpina*
AP1	*VRN1*	*AP1*	–	–
FLC	*VRN2* (*COL* family)	*FLC1*, *FLC2*, *FLC3*, *FLC4*, *FLC5*	*FL1*	*PEP1*
FT	*VRN3*	*FT*	*FT1*, *FT2*	–

(Sung and Amasino 2004b; Kim and Sung 2013, 2014). Nevertheless, the promotion of flowering by vernalization is not exclusively caused by the repression of *FLC*, as plants with a null allele of *FLC* maintain some response to vernalization (Michaels and Amasino 2001), suggesting that other genes are involved. The *MADS AFFECTING FLOWERING 1–5* (*MAF1–5*), which are *FLC* homologs (Ratcliffe et al. 2001, 2003; Scortecci et al. 2001), have been proposed to play a role in the vernalization response; however, their molecular mechanism of action is unknown (Ratcliffe et al. 2003).

Interestingly, several data showed that the extensive allelic heterogeneity at both *FRI* and *FLC* can account for a major fraction of the natural variation in vernalization rate in different *A. thaliana* ecotypes (Johanson et al. 2000; Gazzani et al. 2003; Shindo et al. 2005; Geraldo et al. 2009; Li et al. 2014). *FRI*-like genes with a similar function to *A. thaliana* FRI have been identified in many species, such as *Brassica oleracea*, *A. lyrata*, *Capsella* sp., *Thellungiella halophila*, *Medicago truncatula*, *Lotus japonicus*, *Vitis vinifera*, *Populus balsamífera*, *and Oryza sativa* (Goff et al. 2002; Fang et al. 2008; Kuittinen et al. 2008; Slotte et al. 2008; Risk et al. 2010; Keller et al. 2011; Irwin et al. 2012). Variations in the vernalization responsiveness have been also shown in many of these species (Irwin et al. 2012), suggesting its functional conservation throughout plant evolution. Conversely, *FLC*-like genes as temperature-controlled floral repressors have been identified only in *Arabidopsis*, *Brassica*, *Arabis*, sugar beet (*Beta vulgaris*), and *Petunia* (Michaels and Amasino 1999; Tadege et al. 2001; Schranz et al. 2002; Vandenbussche et al. 2003; Reeves et al. 2007; Wang et al. 2009) (Table 2).

Arabis alpina, a perennial relative of *Arabidopsis*, resumes vegetative growth in fall and repeatedly undergoes vernalization. An *FLC* ortholog [*PERPETUAL FLOWERING 1* (*PEP1*)] acts as a major floral repressor in *Arabis* (Wang et al. 2009). *PEP1* is repressed by vernalizing cold and thus allows plants to bloom. Unlike *Arabidopsis*, *PEP1* is reactivated when plants are returned to warm growth temperature (Kim and Sung 2014). In sugar beet, a pair of *FT* homologs (*BvFT1* and *BvFT2*) acts antagonistically in the floral transition. *BvFT1* acts as a floral repressor whereas *BvFT2* promotes flowering (Pin et al. 2010). Vernalization results in downregulation of *BvFT1*. Vernalization-induced repression of Bv*FT1* is stably maintained even after plants are returned to warm growth temperatures, indicating that *BvFT1* functions similarly to *FLC*. Vernalization requirement in sugar beet is mainly conferred by a dominant allele named *BvBTC1* through its regulation of *BvFT1* and *BvFT2* (Pin et al. 2010). Annual

sugar beet plants with a dominant *BvBTC1* allele do not need vernalization for early flowering. In contrast, biennial sugar beet plants carry a partial loss-of-function allele of *Bvbtc1*. *Bvbtc1* is not significantly induced even under LD without vernalization treatment. *Bvbtc1* allele can be gradually activated by vernalization treatment to the level sufficient to repress *BvFT1* and activate *BvFT2* (Kim and Sung 2014).

Recent studies have revealed that the vernalization pathway emerged from a convergent evolution in dicots and monocots (Amasino and Michaels 2010; Greenup et al. 2011; Ream et al. 2012). In cereals, like wheat or barley, flowering is accelerated by vernalization (by a gene resembling *CONSTANS*), as the change in photoperiod in winter time is a stronger floral determinant than temperature (Dubcovsky et al. 2006). In fact, in rice the flowering pathway is regulated mainly by photoperiod, as it does not present a vernalization requirement (Song et al. 2012b).

Genetic analyses in the temperate cereals wheat and barley have shown that three genes determine the vernalization responsiveness: *VRN1*, *VRN2*, and *VRN3* (Pugsley 1971; Yan et al. 2006). They are, nevertheless, different genes than those with the same name in A. thaliana (Table 2). *VRN1* encodes an *APETALA1*-like MADS-box transcription factor with high similarity to the *A. thaliana* meristem identity genes *APETALA1* (*AP1*), *CAULIFLOWER* (*CAL*), and *FRUITFULL* (*FUL*). *VRN1* is induced after vernalization (Trevaskis et al. 2003; Yan et al. 2003; Oliver et al. 2009; Xiao et al. 2014). *VRN2* is the *A. thaliana FLC* functional analogue, although it belongs to the *COL* gene family (Yan et al. 2004; Higgins et al. 2010). VRN2 is a floral repressor that represses *VRN3*, the ortholog of *A. thaliana FT*, under LD conditions. *VRN2* expression is downregulated after vernalization (Trevaskis et al. 2007). Hence, after vernalization the expression of *VRN1* increases, while *VRN2* expression decreases (Yan et al. 2004). On the other hand, *VRN3* induces *VRN1* in LD conditions (Wigge et al. 2005; Yan et al. 2006). The three genes thus form a regulatory loop. Interestingly, *Arabidopsis* and wheat have different genes, *FLC* and *VRN2*, with the same function. However, vernalization in wheat does not result in significant changes in histone modifications at *VRN2*, suggesting that changes of chromatin structure at *VRN2* locus do not occur. Conversely, induction of *VRN1* in barley is epigenetic; however, the epigenetic changes are the opposite of those in *FLC*. In *VRN1* there is a decrease in H3K27me3, the mark of a transcriptionally inactive gene, and an increase in H3K4me3, a mark of an active gene. Activation of VRN1 is quantitative, with longer cold treatments inducing higher levels of expression (Distelfeld et al. 2009; Oliver et al. 2009, 2013). On the other hand, *Brachypodium* spp. have an ortholog of *VRN1* similar to both wheat and barley that promotes flowering; however, *VRN2* is not conserved in this plant (Ream et al. 2014). Surprisingly, a recent report suggested that an *FLC-like* gene is present in monocots, although its function remains to be investigated (Ruelens et al. 2013).

The epigenetic memory of vernalization is maintained by the PcG proteins in *Arabidopsis*. PcG proteins evolved early in evolution, probably in the common ancestor of animals and plants. As evidenced from the variable copy number of

homologs in plants, diversification of PRC2 subunits occurred only recently in evolution, mostly after the split of monocots and dicots. There are three VEFS domain containing proteins in *A. thaliana*, EMBRYONIC FLOWER2 (EMF2), VRN2, and FERTILIZATION-INDEPENDENT SEED 2 (FIS2), that bestow partially specialized functions on the corresponding PRC2 complexes. In general, there are several copies of *VEF* genes in dicots as well as in monocots; however, the absence of a *VRN2* ortholog in other species (Luo et al. 2009) suggests that PcG function in the regulation of vernalization response evolved especially in Brassicaceae (Derkacheva and Hennig 2014). Nevertheless, it might be possible that a different VEFS gene participates in the vernalization response in other species. Interestingly, three *VIL* homologs have been identified in the einkorn wheat (*Triticum monococcum* L.) (Fu et al. 2007) and in its wild relative *Aegilops tauschii* (Koyama et al. 2012). Of the three *AetVIL* genes, *AetVIL2* was upregulated after 1 week of low-temperature treatment, and its expression pattern was distinct for winter and spring habit accessions. These observations strongly suggest that *AetVIL2* is associated with the vernalization-responsive pathway in *A. tauschii* (Koyama et al. 2012).

3.2 Ambient Temperature

Recent works in *Arabidopsis* have shed some light in the molecular mechanisms underlying the effect of ambient temperatures on flowering time (Verhage et al. 2014). Warm temperature induces flowering in *Arabidopsis* by upregulation of *FT* expression (Halliday et al. 2003; Balasubramanian and Weigel 2006). The acceleration of flowering in response to high temperature requires the activity of PHYTOCHROME INTERACTING FACTOR4 (PIF4) that directly binds to the *FT* promoter in a temperature-dependent manner (Kumar et al. 2012). The PIF4 binding site in the *FT* promoter is occupied by the histone H2A variant H2A.Z, inhibiting its transcription. *FT* expression increases as H2A.Z-containing nucleosomes are evicted in response to high temperatures (Kumar and Wigge 2010; Kumar et al. 2012). Accordingly, mutations of *ACTIN-RELATED PROTEIN6* (*ARP6*) that compromise H2A.Z occupancy cause the warm temperature transcriptome to be constitutively expressed (Kumar and Wigge 2010). However, other plant species respond in an opposite manner to an increase in the ambient temperature or stay largely independent. Therefore, it is important to determine the evolution of these genes and mechanisms to understand plant response to temperature fluctuations. Recent analysis of the genome of *Brassica rapa* revealed the presence of three orthologs of *PIF4* (Song et al. 2014), while two close orthologs of *PIF4* and *PIF5* exist in rice (*Oryza sativa*) (Nakamura et al. 2007), indicating that *PIF4* might be conserved. However, whether there is also a functional conservation cannot be inferred from these genomic data. On the other hand, histone variant H2A.Z is conserved among eukaryotes and has been proposed to mediate warm temperature signals in budding yeast (*Saccharomyces cerevisiae*) as in *Arabidopsis*

(Kumar and Wigge 2010). Therefore, concerning the conservation of the H2A.Z–PIF4 mechanism, H2A.Z is likely not to be the variable factor. As H2A.Z depletion functions as an enabler, rather than an activator of the higher temperature response, transcription factors can differentially regulate gene expression when shifted to a higher temperature. The fact that H2A.Z depletion only provides access to their targets might explain why plants have evolved a different response to increasing ambient temperatures.

Conversely, the MADS-domain proteins FLM and SVP (SHORT VEGETATIVE PHASE) are involved in the suppression of flowering at low ambient temperatures in *Arabidopsis* (Hartmann et al. 2000; Ratcliffe et al. 2001; Scortecci et al. 2001; Werner et al. 2005; Balasubramanian and Weigel 2006; Lee et al. 2007, 2013; Pose et al. 2013). *FLM* (also known as *MAF1*) is a transcription factor that belongs to the *FLC* clade. Interestingly, *FLM* is alternatively spliced under different ambient temperatures. The two main splice forms function antagonistically through interaction with SVP (Balasubramanian and Weigel 2006; Pose et al. 2013). Low ambient temperatures favor the production of the *FLMβ* splice form, whereas more of the *FLMδ* splice form is produced at high ambient temperatures. Both FLMβ and FLMδ interact with SVP. FLMβ–SVP complex binds to DNA as a repressor of flowering. However, the interaction between SVP and FLMδ results in a functionally ineffective complex, leading to the formation of less repressive FLMβ–SVP complexes. In addition, FLMβ–SVP complex is regulated through protein stability of SVP (Lee et al. 2013). SVP protein becomes gradually less abundant as temperature increases from 16 to 27 °C. Decrease in SVP protein leads to a lower abundance of the repressing FLMβ–SVP complex. Therefore, the regulation of FLM isoforms together with the regulation of SVP protein abundance contributes to repress flowering under low ambient temperatures. Interestingly, all *FLC* clade members (*FLM*/*MAF1*, *MAF2*, *MAF3*, *MAF4*, and *MAF5*) are alternatively spliced. However, it seems that *MAF2–MAF4* have evolved different temperature sensitivities (Verhage et al. 2014).

Little is known about the implication of these MADS-box genes in the regulation of flowering time in response to ambient temperature in other species. *FLC*-like genes have been mainly identified as temperature-controlled floral repressors in *Arabidopsis*, *Brassica*, and sugar beet (*Beta vulgaris*) (Michaels and Amasino 1999; Tadege et al. 2001; Schranz et al. 2002; Reeves et al. 2007). Many MADS-box genes have conserved functions across the flowering plants; however, some have acquired novel functions in specific species during evolution. Particularly, the evolution of MADS-box gene subfamilies that control the vegetative-to-floral transition appears to be highly dynamic and linked to the enormous complexity of life history strategies in flowering plants ranging from ephemeral annuals to long-lived trees (Smaczniak et al. 2012a). Future research in other plant species will help to determine whether the orthologs of these or other MADS-box genes have been recruited to this function in other species.

Finally, miR156 and miR172 have been also proposed to regulate floral timing by ambient temperature. Besides timing of the juvenile phase, these two miRNAs have a role in the timing of the phase change from vegetative to reproductive

(Aukerman and Sakai 2003; Wu and Poethig 2006; Verhage et al. 2014). Interestingly, it has been recently shown that miR156-SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 3 (SPL3) module directly regulates *FT* expression in the leaf to control ambient temperature response to flowering. Overexpression of miR156 leads to more delayed flowering at a lower ambient temperature (16 °C), which has been associated with downregulation of *FT* and *FUL* expression. Among miR156 target genes, *SPL3* mRNA levels are significantly reduced at 16 °C. Overexpression of miR156-resistant *SPL3* causes early flowering, regardless of the ambient temperature. Furthermore, SPL3 protein directly binds to GTAC motifs within the *FT* promoter. These data suggest that the interaction between the *miR156–SPL3* module and *FT* is part of the regulatory mechanism controlling flowering time in response to ambient temperature (Kim et al. 2012). Conversely, a higher miR172 expression was observed at 23 °C than at 16 °C (Lee et al. 2010). Both miR156 and miR172 belong to a subset of evolutionary conserved miRNAs that are present throughout the angiosperms (Axtell and Bowman 2008; Cuperus et al. 2011). Results obtained in different dicots and monocots indicate that these miRNAs are not only conserved in sequence but also in their role in regulating phase transition. In addition, mature miRNA has been detected in various mosses, ferns, and gymnosperms (Arazi et al. 2005; Zhang et al. 2006; Axtell and Bowman 2008; Cuperus et al. 2011). In contrast to miR156, miR172 appears to be angiosperm specific, and it has not been cloned from other land plants (Axtell and Bowman 2008; Cuperus et al. 2011), even though the expression of miR172 has been detected by microarrays of RNA extracted from ferns (Axtell and Bowman 2008) and has been computationally predicted in *Physcomitrella* (Fattash et al. 2007). However, whether these miRNAs have a role in controlling thermosensory flowering time in other plants remains to be investigated.

4 Nutrients Signaling to Flowering

Sugars are the main source of carbon and energy for most cell types. For that reason, sugars have been recruited as key regulators of metabolic processes, but they are also involved in the regulation of many other physiological and developmental processes. Its widespread function has contributed to the increase in diversification and plasticity of higher eukaryotes, a phenomenon that acquires an enormous importance in photosynthetic and sessile organism like plants. Therefore, plants have developed more complex and flexible regulatory mechanisms than the rest of higher eukaryotes, and one of such processes is flowering (Rolland et al. 2006). In unicellular algae, routes controlled by sugars are poorly known, and sugar sensing has been involved in metabolic processes such as amino acid transport and astaxanthin biosynthesis in *Chlorella* (Kato and Imamura 2008; Li et al. 2008).

While temperature and photoperiodic signals are key external factors in the *Arabidopsis* floral transition, internal factors such as hormones, nutrients, or plant

age have also a strong influence on flowering time (Amasino 2010; Fornara et al. 2010). However, the connection between carbohydrates and flowering is not entirely understood. There are numerous physiological studies showing the effect of sugars in flowering time in different species (Bernier et al. 1993; Lebon et al. 2008), although it is not clear whether they act to promote flowering (Corbesier et al. 1998; Roldan et al. 1999; Wahl et al. 2013) or as floral inhibitors (Zhou et al. 1998; Ohto et al. 2001). The induction of flowering is also associated with the mobilization of starch reserves and a transient increase in carbohydrate transport to the shoot apical meristem (SAM) during the floral transition (Corbesier et al. 1998). Recent studies have shown that this mechanism is controlled by CO, the central photoperiod regulator (Ortiz-Marchena et al. 2014). Interestingly, this process seems to be conserved throughout evolution, as the ancestral CO homolog, CrCO, is also involved in the photoperiodic control of starch accumulation in *Chlamydomonas* (Serrano et al. 2009; Romero and Valverde 2009; Valverde 2011).

It has been shown that trehalose-6-phosphate (T6P) affects flowering in *Arabidopsis* WT plants, so that an increase in sucrose during the floral transition would be signaled by an increase in T6P (Wahl et al. 2013). Plants with abnormal levels of T6P have altered flowering time. Thereby, high levels of T6P would induce the floral transition and vice versa (Schluepmann et al. 2003; Wahl et al. 2013). *FT* expression is reduced in plants with low amount of T6P, so it could be possible that T6P promotes flowering through activation of the florigen (Wahl et al. 2013). Therefore, it has been suggested that T6P promotes flowering when carbohydrate levels are high, influencing the photoperiod pathway (Tsai and Gazzarrini 2014). In this sense, T6P signal could affect flowering through miR156 and SPL (Matsoukas et al. 2012), so that T6P inhibits *miRNA156* expression and SPL is then able to promote the floral transition (Wahl et al. 2013). Although in green algae T6P regulatory function is unknown, its biosynthetic mechanism is conserved in all algae and even in bacteria (Avonce et al. 2010; Michel et al. 2010; Deng et al. 2014; Pade et al. 2014).

In plants, transcriptional regulation by sugars interacts with signaling pathways mediated by hormones, although the mechanism by which this occurs is unknown. Evidence suggests that it is probably due to direct interactions between protein components of both routes in complexes, although there may also be indirect interactions (Gibson 2004; Jossier et al. 2009). Hexose levels, such as glucose and fructose, for example, are sensed by HEXOKINASE1 (HXK1). HXK1 is a glucose-phosphorylating enzyme that exerts a dual function as sugar sensor and hexose kinase. Both functions are independent, so that the metabolism of the hexose phosphate is not involved in the signaling function (Loreti et al. 2000; Moore et al. 2003; Valverde et al. 2005). The conservation of some steps in the signal cascade of sugar sensing is still in controversy. However, HXK is considered a conserved glucose sensor among algae, yeast, plants and animals (Pego et al. 2000; Li et al. 2008; Oesterhelt and Gross 2014).

Two other important systems regulate sugar signaling in plants, the Snf1-related kinase 1 (SnRK1) and the target of rapamycin (TOR) kinase. Both of them are central regulators that sense nutrient levels and promote or inhibit growth in an

antagonistic way: low sugar levels promote *SnRK1* expression and high sugar levels upregulate TOR activity (Deprost et al. 2007; Smeekens et al. 2010; Robaglia et al. 2012). Although there are two possible orthologs of *SnRK1* annotated in the *Chlamydomonas* genome, there is no evidence about its functions. However, TOR is a central regulator of cell growth in all eukaryotes (Crespo 2012), and *Chlamydomonas* is no exception as TOR is regulated by nutrients (Crespo et al. 2005). Recently, T6P has been shown to inhibit SnRK1 activity in *Arabidopsis* (Zhang et al. 2009). T6P seems to have this function also in monocots, indicating a conserved role for this sugar (Zhang et al. 2009; Wu and Birch 2010; Debast et al. 2011; Martinez-Barajas et al. 2011; Nunes et al. 2013; Lawlor and Paul 2014). Both T6P and SnRK1 have opposite functions as major regulators of gene expression related to growth and energy (Baena-González and Sheen 2008; Zhang et al. 2009).

It has also been reported in *Arabidopsis* that *EXORDIUM* (*EXO*) and *EXO-LIKE* genes control growth on different environmental conditions through the response to brassinosteroids (Schroder et al. 2009). EXO proteins seem to modify the response to sugars in seedlings and to control general gene expression by sugars and the accumulation of starch mediated by sugars, ABA, and anthocyanins. Therefore, EXO protein would establish a balance between the levels of external carbon available for plant and the cell status (Lisso et al. 2013). In green algae, it has been shown that brassinosteroids and auxins work synergistically in the control of growth and metabolism (Bajguz and Piotrowska-Niczyporuk 2013), but until now, no *EXO* homolog has been described in any algal genome.

All these premises suggest that sugar sensing is an ancient, flexible regulatory mechanism that evolved, using ancestral elements, according to the needs of each organism.

Although sugars play an important role in the floral transition, nitrogen (N) availability also influences flowering time (Frink et al. 1999). N is an essential macronutrient and specifically N deprivation induces early flowering in different plants including *Arabidopsis* (Dickens and Staden 1988; Bernier et al. 1993; Loeppky and Coulman 2001; Castro Marin et al. 2011; Kant et al. 2011; Liu et al. 2013). Under N deprivation, the flowering integrators *FT*, *AP1*, and *LEAFY* (*LFY*) are induced (Kant et al. 2011). Also, *CO* expression is induced in low nitrate conditions and is repressed by high nitrate levels (Liu et al. 2013). On the other hand, spray of nitrate to stem and leaves induces flowering formation in mango trees in the tropics (Núñez-Elisea and Caldeira 1988). N also governs many processes in algae. In *Chlamydomonas*, N controls sexual life cycle (Goodenough et al. 2007), photosynthesis (Grossman 2000), and lipid induction (Sharma et al. 2012), among other processes. Nevertheless, the general regulatory mechanisms that connect N metabolism to developmental responses are widely unknown.

5 Flower Development

Floral organogenesis is a natural extension of the floral transition process and shares many early genes involved in SAM differentiation and tissue organization. Floral integrators such as *FT*, *AP1*, and *LFY* have a significant role in the early stages of floral tissue formation, and their mutation aborts the early differentiation process of the vegetative apical meristem into a reproductive meristem. In fact, flower appearance is extremely variable among species in size, shape, symmetry, and pigmentation, although the different whorls of organs originate from the floral meristem, a small group of undifferentiated cells. Typical angiosperm flowers consist of four organ types arranged in four concentric whorls at the tip of a floral shoot. From the outside to the inside of the flower, these organs are leaflike green sepals (whorl 1), generally colored petals (whorl 2), the male reproductive organs or stamens (whorl 3), and carpels (whorl 4), the female reproductive organs. During their life cycle, plants undergo several phase transitions in which miR156 and miR172 play an important role (Huijser and Schmid 2011; Poethig 2013; Wu and Poethig 2006). Among them, the vegetative-to-reproductive phase transition ends up with the formation of the flower. During this transition, the SAM changes to an inflorescence meristem (IM). The IM can be converted in a floral meristem (FM) or produce lateral meristems that will be, in turn, converted in a FM. The FM undergoes an early growth phase before the identity of the floral organs is established (McKim and Hay 2010). The characterization in *Arabidopsis thaliana* and *Antirrhinum majus* of different homeotic mutants in which the identity of floral organs was altered leads to the proposal of the ABC model for flower development (Haughn and Somerville 1988; Sommer et al. 1990; Coen et al. 1990, 1991; Yanofsky et al. 1990; Coen 1991; Carpenter and Coen 1990; Coen and Meyerowitz 1991; Schwarz-Sommer et al. 1990; Bowman et al. 1991). These homeotic mutants defined three overlapping functions, A, B, and C (Fig. 3), each operating in two adjacent whorls that specify the identity of the four floral organ types (Coen and Meyerowitz 1991). A-function mutants display carpels in the first whorl and stamens in the second whorl instead of sepal and petals, respectively. B-function mutants have sepals in the second whorl and carpels in the third whorl rather than petals and stamens. Finally, in C-function mutants petals substitute stamens in the third whorl and sepals carpels in the fourth whorl. Besides, C-function mutants are indeterminate and produce floral organs inside the fourth whorl. The A function acts alone in the outermost whorl (whorl 1) to specify sepal identity. A and B functions act in the second whorl to specify petals. The reproductive organs are specified by the action of B and C functions. Thus, stamens are determined by the joint action of B and C functions in the third whorl. At the center of the flower, in whorl 4, the C function acts alone to initiate carpel development and to terminate further development of the floral meristem. The ABC model also proposes that activity of C and A functions is mutually exclusive and C function is restricted to the third and fourth whorls by A function and vice versa (Fig. 3) (Coen and Meyerowitz 1991). Most floral homeotic genes controlling floral organ identity

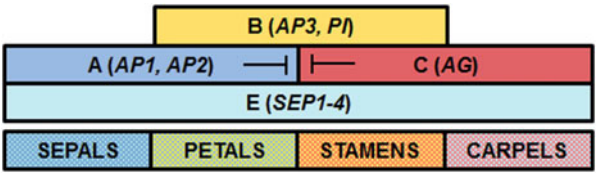

Fig. 3 Specification of floral organ identity. The combination of A, B, C, and E functions originates the specification of the four organ types. *Arabidopsis* genes responsible for the corresponding functions are indicated inside the expression domains of each function in a color-coded pattern

encode MADS-box transcription factors (Meyerowitz 1997; Ng and Yanofsky 2001; Theissen 2001; Schwarz-Sommer et al. 1990; Krizek and Fletcher 2005; Lohmann and Weigel 2002; Jack 2001). MADS is an acronym for *MCM1* (yeast), *AGAMOUS* (*Arabidopsis*), *DEFICIENS* (*Antirrhinum*), and *SRF* (human) on which the definition of this gene family was based (Schwarz-Sommer et al. 1990).

5.1 Floral Identity Determination

Plant floral meristem identity genes control floral meristem versus shoot/inflorescence fate (Bartlett et al. 2008). The meristem identity genes *LFY* and *AP1* in *Arabidopsis* and *FLORICAULA* (*FLO*) and *SQUAMOSA* (*SQUA*) in *Antirrhinum* induce flower development, whereas *TERMINAL FLOWER1* (*TFL1*) in *Arabidopsis* and *CENTRORADIALIS* (*CEN*) in *Antirrhinum* promote inflorescence development (Blazquez et al. 2006; Bradley et al. 1996; Alvarez et al. 1992; Coen et al. 1990; Huijser et al. 1992; Weigel et al. 1992; Mandel et al. 1992). Meristem identity genes are responsible for the determination of the floral meristem at the SAM for the control of the floral organ identity functions (mainly *MADS*-box genes). This transition represents the first step specific to floral development and is driven by the *FLO*/*LFY* genes. *flo* and *lfy* mutants produce proliferating inflorescence shoots instead of flowers (Coen et al. 1990; Schultz and Haughn 1991; Weigel et al. 1992). Homologs to *FLO*/*LFY* have been identified in many different plants and are present in most of the terrestrial plants analyzed, including mosses, ferns, gymnosperms, and angiosperms (Maizel et al. 2005).

The flowering signaling pathways responding to environmental, autonomous, and endogenous signals converge in the so-called floral integrators. *FT–FD* complex at the SAM induces flowering by activating *SUPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*), which in combination with *AGAMOUS-LIKE 24* (*AGL24*) promotes the expression of the floral meristem identity gene *LFY* (Lee et al. 2008), which in turn will directly induce the expression of *AP1* (Mandel and Yanofsky 1995; Parcy et al. 1998; Wagner et al. 1999). The *FT–FD* complex also directly activates *AP1* originating a feed-forward loop. Induction of *LFY* is also mediated by a set of different genes as *SHOOT*

MERISTEMLESS (*STM*), *PENNYWISE* (*PNY*), *POUND-FOOLISH* (*PNF*), and *SPL3* that activate *LFY* and thus the transition to FM (Yamaguchi et al. 2009; Lee et al. 2008; Kanrar et al. 2008; Smith et al. 2011; Pose et al. 2012; Wigge et al. 2005).

Although *LFY* is considered to be the main actor of this transition, other transcription factors from the MADS-box family as *FUL* and *AP1* are also necessary (Ferrandiz et al. 2000; Melzer et al. 2008; Bowman et al. 1993; Mandel and Yanofsky 1995; Weigel and Nilsson 1995) and are co-regulated with *LFY* by *SPL3* (Yamaguchi et al. 2009; Huijser and Schmid 2011). *LFY* and *AP1* control the whole floral network regulating genes involved in the determinacy of the floral meristem and floral organ primordia (Coen et al. 1990; Benlloch et al. 2007; Weigel et al. 1992; Moyroud et al. 2009, 2010; Liu et al. 2009; Irish 2010) and constitute hubs that coordinate multiple processes and developmental pathways (O'Maoileidigh et al. 2014). *LFY* codes for a plant-specific transcription factor that is present as a single-copy gene in most angiosperms and binds to the regulatory regions of its target genes as a dimer with a DNA-binding domain structurally similar to the helix–turn–helix domain (Maizel et al. 2005; Benlloch et al. 2007; Hames et al. 2008; Parcy et al. 1998; Busch et al. 1999; Lamb et al. 2002; Lohmann et al. 2001; Moyroud et al. 2009). *LFY* is expressed at low levels in vegetative tissues, is upregulated in response to the flowering signals, and is expressed in the floral organ primordial where it participates in establishing specific gene expression patterns in the floral organ primordia.

Angiosperms evolved from gymnosperm ancestors at least 130–136 MYA, as evidenced by the earliest fossilized record of pollen from an apparent angiosperm known to date (Frohlich 2006). During plant evolution, several genome duplication events have occurred. However, as indicated before, *LFY* in angiosperms is a single-copy gene in most species with the exception of maize and Lamiales (Aagaard et al. 2006; Bomblies et al. 2003); thus, *LFY* can provide evidences on the evolutionary pace of plants. Some species exhibit various *LFY*-like genes that have been shown to be paralogs acquired recently by polyploidy as in *Nicotiana tabacum* or from small-scale duplication events (Moyroud et al. 2009). On the other hand, gymnosperms usually present two paralogs, *LFY* and *NEEDLY* (*NDLY*) (Mellerowicz et al. 1998; Mouradov et al. 1998), originated in a gymnosperm-specific duplication, with the *NDLY* lineage being lost in angiosperms (Frohlich and Estabrook 2000; Maizel et al. 2005; Himi et al. 2001; Frohlich 2003). Gymnosperm *LFY* homologs are mainly expressed in reproductive meristems and are able to complement *Arabidopsis lfy* mutants, indicating that LFY function is conserved between gymnosperms and angiosperms (Mouradov et al. 1998; Shindo et al. 2001; Maizel et al. 2005). Homologs of *LFY* have also been identified in ferns, mosses, and thallophytic green algae (Himi et al. 2001; Tanahashi et al. 2005; Sayou et al. 2014). Fern *LFY* homolog *CrLFY2* can partially rescue the *Arabidopsis lfy* phenotype (Maizel et al. 2005). In the moss *Physcomitrella patens*, two *LFY* homologs have been identified (*PpLF1*, 2) that have been shown to regulate cell division in the zygote (Tanahashi et al. 2005). PpLFY1 is unable to bind the

sequence recognized by *Arabidopsis* LFY, although one amino acid substitution is sufficient for binding to a canonical LFY binding site (Maizel et al. 2005).

By analyzing the binding specificity of LFY homologs from different groups of plants, including green algae, it has been suggested that during evolution LFY modified its DNA binding specificity even though plant genomes generally contain a single *LFY* copy (Sayou et al. 2014). Gene duplication followed by sub-functionalization is a common mechanism in evolution. Duplicated genes loose the obligation to maintain its original function and can evolve to acquire new functions through mutations in their regulatory or coding regions. However, in the case of *LFY*, the acquisition of the floral function seems to be related to changes in its DNA-binding domain (and probably in the cis-regulatory elements of its target genes) through an intermediate showing various binding specificities, thus avoiding deleterious effects (Sayou et al. 2014; Maizel et al. 2005; Della Pina et al. 2014; Kovach and Lamb 2014). The fact that *LFY* is present in multicellular and not in unicellular algae and that it is related to meristem organization suggests that *LFY* is associated to multicellularity, in contrast to *COLs*, *DOFs*, *bHLHs*, and other families of regulatory genes that originated in unicellular algae (Serrano et al. 2009; Romero-Campero et al. 2013).

5.2 *Floral Organ Identity Determination*

As indicated above, the floral meristem identity genes control the floral organ identity genes, whose mutation induces homeotic transformation of one organ into another. Genes that contribute to the A, B, and C functions are transcription factors and are known in different plants. In the case of *Arabidopsis*, AP1 and *APETALA2* (*AP2*) are A-function genes, *APETALA3* (*AP3*) and *PISTILLATA* (*PI*) are B-function genes, and AGAMOUS (AG) is a C-function gene (Fig. 3) (Theissen 2001). The ABC function genes belong to the MADS-box family of transcription factors, with the exception of AP2, which belong to the AP2/ERF family (Jofuku et al. 1994; Weigel 1995; Okamuro et al. 1997; Riechmann and Meyerowitz 1998). The ABC model has been implemented by the identification and characterization of four MADS-box SEPALLATA genes (SEP1–4), which act redundantly and are required for the A, B, and C functions (Pelaz et al. 2000; Ditta et al. 2004), giving rise to the ABCE model for flower development (Wellmer et al. 2014; Theissen 2001). The ABCE functions would act in a combinatorial manner to specify each of the four floral organs. Thus, class A and E genes are necessary to specify sepals; class B and E genes are necessary to specify petals; class B, C, and E genes specify stamens; and finally class C and E genes specify carpels (Fig. 3) (Theissen 2001; Ditta et al. 2004; Theissen and Melzer 2007a).

According to the ABCE model, floral organ determination is accomplished by the formation of multimeric complexes of floral organ identity proteins that bind to two CArG boxes with a consensus sequence $CC(A/T)_6GG$ (Wynne and Treisman 1992; Honma and Goto 2001). Analysis of the interaction between DEFICIENS

(DEF), GLOBOSA (GLO), and SQUAMOSA (SQUA) from *Antirrhinum majus* provided the first evidences on the establishment of tetramers composed of a heterodimer DEF–GLO and a homodimer SQUA–SQUA (Egea-Cortines et al. 1999). *DEF*, *GLO*, and *SQUA* are the orthologs of *Arabidopsis AP3*, *PI*, and *AP1*, respectively (Becker and Theissen 2003). Based on the observation that the SEP genes are also involved in the formation of petals, stamens, and carpels (Pelaz et al. 2000) and act as mediators of higher-order complex formation, the floral quartet model was coined as a mechanistic model for the determination of floral organs (Theissen and Saedler 2001; Honma and Goto 2001; Wellmer et al. 2014; Theissen and Melzer 2007b; Melzer and Theissen 2009; Erdmann et al. 2010; Melzer et al. 2009; Jetha et al. 2015). The floral quartet model indicates that specification of floral organs is mediated by the combinatorial formation of tetramers of MADS-domain proteins, although it has also been shown that floral organ identity MADS-box proteins interact with other types of proteins as chromatin-associated proteins and other transcription factors to establish higher-order complexes (Smaczniak et al. 2012a, b; Wellmer et al. 2014; O'Maoileidigh et al. 2014; Simonini et al. 2012; Liu et al. 2009).

MADS-box genes constitute a large family that has been divided in two main lineages, type I and type II, which are present in plants, animals, and fungi (Alvarez-Buylla et al. 2000a). Members of the MADS-box transcription family are characterized for the presence of a highly conserved MADS-box with a length of about 180 nucleotides that codes for the DNA binding to the CArG box (Alvarez-Buylla et al. 2000b; Theissen et al. 2000; Riechmann and Meyerowitz 1997). The MADS-box genes in plants, with more than 100 members, were initially implicated in floral organ specification, although it has been shown to participate in many different developmental processes during the life cycle of plants (Smaczniak et al. 2012a; De Bodt et al. 2005). The family of MADS-box genes increased considerably during evolution by duplication-divergence-specialization of individual paralogs. Type I MADS-box genes form a heterogeneous group that just share the MADS domain (Kofuji et al. 2003; Parenicova et al. 2003; De Bodt et al. 2003). Type I and II MADS-box genes have been identified in all land plant lineages, from bryophytes to angiosperms. Their number and their functional diversity increased considerably during evolution (Becker and Theissen 2003; Kramer and Hall 2005; Kaufmann et al. 2005; Gramzow and Theissen 2010). Recently, several type I MADS-box genes have been shown to have regulatory roles in different aspects of plant reproduction as female gametogenesis and seed development (Masiero et al. 2011; Portereiko et al. 2006; Steffen et al. 2008; Kang et al. 2008). It has also been suggested that type I MADS-box proteins form heteromeric complexes (de Folter et al. 2005). The MADS-box type II lineage includes the floral homeotic genes as well as genes participating in embryogenesis, flowering time, and fruit development, among others (Smaczniak et al. 2012a). Type II MADS-box genes are characterized for having an N-terminal MADS domain, an intervening domain (I) and a keratin-like domain (K) that are essential for protein–protein interaction, and a very variable C-terminal domain, thus named MIKC-type MADS-box (Kaufmann et al. 2005; Smaczniak et al. 2012a). MIKC-type has been subdivided

in two groups, MIKCc and MIKC*, the latter generally having a longer K domain (Henschel et al. 2002; Kwantes et al. 2012; Smaczniak et al. 2012a), that have been characterized in seed plants, pteridophytes, and mosses, indicating that the two groups diverged before the separation of mosses and land plants. In the unicellular green and red algae *Chlamydomonas reinhardtii* and *Cyanidioschyzon merolae*, respectively, a single MADS-box gene, lacking the I, C, and K domains, has been identified (Tanabe et al. 2005). However, MIKC-type MADS-box genes have been characterized in charophycean green algae, having a role in haploid reproductive development during the gametophytic phase (Tanabe et al. 2005). Land plants originated from multicellular charophycean algae about 500 MYA (Graham et al. 2000); thus, MIKC-type MADS-box genes might be recruited to form higher-order complexes before the origin of land plants. The fact that all the charophycean algae MADS-box genes characterized belong to the MIKCc type indicates that they are ancestral to the MIKC* type (Tanabe et al. 2005) and that MICK*-type genes evolved in the charophycean–land plant lineage after its divergence from *Chlamydomonas*. Considering that mosses and club moss (lycophyte) (Henschel et al. 2002), and the rest of land plant lineages, have both types of MIKC genes, it can be assumed that the last common ancestor of mosses and land plants (about 450 MYA) already had both types of MIKC MADS-box genes.

MADS-box genes are generally associated with the development of reproduction in extant land plant, mosses, and green algae relatives. However, extensive duplication events followed by specialization gave rise to a plethora of MADS-box genes involved in many different aspects of plant life cycle other than reproductive processes (Smaczniak et al. 2012a). Many different target genes involved in transcriptional and cellular signaling have been identified for FLC, SEP3, and AP1 (Deng et al. 2011; Kaufmann et al. 2009, 2010; Ito 2011; Dornelas et al. 2011), so the complexity of MADS-box transcription factors at the level of number of members, functions, spatiotemporal expression, posttranscriptional regulation, establishment of high-order complexes, and their putative role in more than organ or developmental stage will require the use of massive analysis techniques to generate a global framework to understand the evolution of this transcription factor family. Besides, the characterization of gene regulatory networks (GRN) will also provide primordial information to the study of MADs-box genes (Espinosa-Soto et al. 2004; van Mourik et al. 2010).

6 Conclusions

The study of the flowering pathways during the evolutionary history of plants unveils regulatory aspects that cannot be deduced from the study of single stories within the same species. We have learned that some of these regulatory pathways are conformed by a set of evolutionarily conserved genes that share even the same hierarchical regulatory mechanisms and modules. These “toolkits” were present as simple, short pathways in unicellular algae and evolved to long, complex ones in

angiosperms. The addition of gene copies and new regulatory modules seem to have been a constant in many of the flowering pathways that allowed modern plant to respond with high efficiency to changing environmental conditions. This plasticity is essential to assure that flowering, and thus seed release, will be planned ahead and triggered at the moment of the year that guarantees a successful offspring for the species. This is of course intertwined with other signals such as the synchronicity with pollinator's signals and competing species that are too complex to discover in a direct analysis, but perhaps will become easier to understand if we learn to identify the gene toolkits and basic mechanism that rule these transitions.

The advent of massive analysis techniques is allowing us the rigorous and systematic study of non-model plant species. This information is being fed to computational analysis built upon the regulatory pathways constructed in model species. Surprisingly, these analyses have revealed a lot of homogeneity in the flowering pathways even among very different plant families. Therefore, it seems plausible to believe that these signaling mechanisms were mastered in the early flowering plants, were recruited from mechanisms that triggered developmental decisions in primitive plants, and have thus remained relatively unchanged during evolution due to their importance. This evolution and development perspective could allow us to better understand the response of plants to the incoming changing environmental conditions, intensified by human activity, and develop strategies to make plants flower at the correct time of the year in order to better perpetuate their species and ours.

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