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Recent advancements to study flowering time in almond and other Prunus species

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Flowering time is an important agronomic trait in almond since it is decisive to avoid the late frosts that affect production in early flowering cultivars. Evaluation of this complex trait is a long process because of the prolonged juvenile period of trees and the influence of environmental conditions affecting gene expression year by year. Consequently, flowering time has to be studied for several years to have statistical significant results. This trait is the result of the interaction between chilling and heat requirements. Flowering time is a polygenic trait with high heritability, although a major gene Late blooming (Lb) was described in “Tardy Nonpareil.” Molecular studies at DNA level confirmed this polygenic nature identifying several genome regions (Quantitative Trait Loci, QTL) involved. Studies about regulation of gene expression are scarcer although several transcription factors have been described as responsible for flowering time. From the metabolomic point of view, the integrated analysis of the mechanisms of accumulation of cyanogenic glucosides and flowering regulation through transcription factors open new possibilities in the analysis of this complex trait in almond and in other Prunus species (apricot, cherry, peach, plum). New opportunities are arising from the integration of recent advancements including phenotypic, genetic, genomic, transcriptomic, and metabolomics studies from the beginning of dormancy until flowering.

Keywords: Prunus dulcis, breeding, almond, flowering time, dormancy, genome, transcription factors, molecular markers

INTRODUCTION

From a commercial point of view, flowering time is one of the most important agronomic traits in almond (Prunus dulcis (Miller) D. A. Webb) as it determines the vulnerability of production to late frosts, as well as the use of cultivars for cross-pollination in order to achieve successful pollination when the flowering time of two varieties must coincide (Dicenta et al., 2005).

Breeding new, late flowering almond cultivars is a very long and costly task since, due to the long juvenile period, their first flowering usually occurs in the third year after plantation in the field, or even later. In addition, the influence of climatic factors on this trait obligates the breeder to record the data for several years (Dicenta et al., 1993, 2005). In this sense, it would be very useful to have tools for early selection of the latest flowering seedlings in the nursery (after germination of seeds), which would be planted in the experimental orchards for further selection (Dicenta et al., 2005). Flowering will only happen when dormancy is broken. Endodormancy has been described as the inability of a tree to start floral or vegetative budbreak, even with moderate temperatures. Endodormancy occurs prior to ecodormancy, which happens in late winter and spring and is imposed by temperatures unfavorable to growth (Sánchez-Pérez et al., 2012).

On the other hand, almond and other Prunus species (apricot, cherry, peach, plum, etc.) accumulate a mono cyanogenic glucoside (CNGLc) called prunasin in different vegetative and reproductive parts of the plant, and in the seeds a di-CNGLc called amygdalin (McCarty et al., 1952; Frehner et al., 1990; Sánchez-Pérez et al., 2008). When specific enzymes called β-glucosidases degrade CNGLcs, glucose, benzaldehyde and cyanide are released (Morant et al., 2008). Upon degradation of hydrogen cyanamide—a nitrogen-based chemical compound sprayed in the flower buds—nitroxil and cyanide are released. This brings forward the flowering time in apple, apricot, peach, persimmon, sweet cherry flower buds, etc., when compared to untreated plants (Dozier et al., 1990; George et al., 1992; Faust et al., 1997).

In this work, recent advancements to study flowering time in almond have been included at the phenotypic (observed trait), genetic (inheritance and transmission), genomic (DNA analysis), transcriptomic (gene expression analysis) and metabolomic (metabolites involved, as cyanide content) level.

PHENOTYPIC STUDIES

In general, the accuracy of phenotypic evaluation is critical for further reliable genetic and molecular studies. To diminish the significant influence of the environment, flowering time can be dissected as the sum of two traits: chilling and heat requirements. These can be determined in monitored conditions by measuring the temperatures in the field and simultaneously controlling temperatures and humidity in the growth chamber (Egea...
et al., 2003; Sánchez-Pérez et al., 2012). Chill requirements have a much stronger effect on flowering time compared to heat requirements (Egea et al., 2003) with a high positive correlation between chilling requirements and flowering time (Sánchez-Pérez et al., 2012).

These results were also verified in other Prunus species such as apricot (P. armeniaca L.) (Ruiz et al., 2007) and sweet cherry (P. avium L.) (Alburquerque et al., 2008). However, Alonso et al. (2005) described a higher influence of heat requirements than chilling requirements on the flowering time in cold areas, using a mathematical model recording temperatures and flowering time, but not evaluating the endodormancy breaking in flower buds.

**GENETIC STUDIES**

Inheritance studies of the genetic control of flowering time on almond showed that flowering time is a polygenic trait (Kester et al., 1977; Dicenta et al., 1993; Sánchez-Pérez et al., 2007a). However, a major dominant gene controlling this trait was described specifically in some descendants of the almond cultivar “Tardy Nonpareil,” considered a late flowering mutant of “Nonpareil” (Kester, 1965; Socias i Company et al., 1999; Sánchez-Pérez et al., 2007a). These authors, studying some descendants of “Tardy Nonpareil,” observed a bimodal distribution for this trait, which was explained by the presence of a late blooming major gene (late blooming, Lb), quantitatively modified by minor genes.

Flowering time of almond has a high heritability (Kester et al., 1977; Dicenta et al., 1993), so crossing late-flowering parents will produce late-flowering seedlings (Dicenta et al., 2005). The best breeding strategy to obtain late-blooming almond descendants is therefore to cross parents as late-blooming as possible, and when the offspring shows a bimodal distribution, the latest-blooming genotypes should be selected, probably carrying the Lb allele, which could be transmitted to its descendants (Sánchez-Pérez et al., 2012).

On the other hand, studies on the genetic basis and inheritance of chilling and heat requirements to break endodormancy and ecodormancy in almond are scarcer. Sánchez-Pérez et al. (2012) described a polygenic nature of these traits in accordance with the observed flowering time of seedlings. In addition, these authors observed, in a 2-year study, that the bimodal distribution of chilling requirements in the studied progeny could be explained by the presence of the Lb gene hypothetically linked to these chilling requirements. In other Prunus, quantitative inheritance of chilling requirements for breaking endodormancy and ecodormancy in almond are scarcer. Sánchez-Pérez et al. (2012) described a polygenic nature of these traits in accordance with the observed flowering time of seedlings. In addition, these authors observed, in a 2-year study, that the bimodal distribution of chilling requirements in the studied progeny could be explained by the presence of the Lb gene hypothetically linked to these chilling requirements. In other Prunus, quantitative inheritance of chilling requirements for breaking endodormancy and ecodormancy in almond are scarcer. Sánchez-Pérez et al. (2012) described a polygenic nature of these traits in accordance with the observed flowering time of seedlings. In addition, these authors observed, in a 2-year study, that the bimodal distribution of chilling requirements in the studied progeny could be explained by the presence of the Lb gene hypothetically linked to these chilling requirements.

The first genomic studies performed used RAPDs (Random Amplified Polymorphic DNA) and bulk segregant analysis in a F1 progeny from “Tardy Nonpareil,” corroborating the presence of the previously mentioned major gene Lb controlling late flowering time. Moreover, three RAPDs were found to be associated with Lb in linkage group 4 (G4) of the “Felisia” × “Bertina” (“Felisia” is a descendant from “Titan,” that is a seedling of “Tardy Nonpareil”) genetic map (Ballester et al., 2001). In addition, Silva et al. (2005) described several Quantitative Trait Loci (QTLs) linked to flowering time in an interspecific F1 almond × peach progeny using a Candidate Gene approach (CG) in G1, G2, G3, G5, G6, and G7. More recently, different works using SSR (Simple Sequence Repeat) markers in a F1 population between a seedling of “Tardy Nonpareil” (“R1000”) × “Desmayo Largueta” (R×D), also confirmed the location of Lb in G4 and identified other QTLs
to flowering time in G1, G6, and G7 (Sánchez-Pérez et al., 2007b; Martínez-Gómez et al., 2012) (Figure 1). In the first study (2007), carried out in this RxD population, the SSR UDP-96003 was located very close to the \( Lb \) gene in G4 of the map. When QTL analysis was performed, this major QTL (\( Lb \)) in G4 was able to explain between 56.5 and 86.3% of the variance in “R1000,” which is supposed to carry the \( Lb \) gene, and 54.5–67.7% of the variance in the mapped RxD population.

In other \( Prunus \) species, QTLs associated with flowering time were also described in peach, apricot and cherry, confirming the polygenic nature. In peach, Fan et al. (2010) described different QTLs linked to flowering time in G1, G2, G4, G6, G7, and G8. Campoy et al. (2011) and Salazar et al. (2013) described a QTL linked to flowering time in G1, G5, and G7 in apricot. Finally, Wang et al. (2000); Dirlewanger et al. (2012), and Castede et al. (2014) also identified a QTL linked to flowering time in G1, G2, and G4 of sour and sweet cherry.

Silva et al. (2005) and Sánchez-Pérez et al. (2012) described several QTLs linked to chilling and heat requirements in G1, G2, G4, G6, G7, and G8 in peach. QTLs linked to chilling requirements of vegetative buds were described in apricot by Oluoku et al. (2009) in G1, G2, G3, G5, and G8. In sweet cherry (\( P. avium \)), Dirlewanger et al. (2012) and Castede et al. (2014) also found one QTL in G4 in sweet cherry.

Moreover, functionally characterized homologs from \( Arabidopsis \) were used as a CG approach with 10 genes from \( Arabidopsis \) (\( PrdTFL \), \( PrdGA20 \), \( PrdLFY \), \( PrdAP1 \), \( PrpAP2 \), \( PrpCO \), \( PrpFT \), \( PrpAGL2 \), \( PrpFAR1 \), \( PrdTFL \), \( PrdGA20 \), \( PrpAP2 \), and \( PrpCO \)) (Silva et al., 2005). These 10 genes were mapped in the \( Prunus \) reference map (Texas x Earlygold) and can be found in G1, G2, G3, G5, G6, and G7 (Figure 1, Table 1). However, none of them co-localized with \( Lb \) gene in G4. One reason for this is that there are more than 60 genes involved in flowering time in \( Arabidopsis \), so other CGs should be analyzed. The other reason could be that the flowering time trait is due to different mechanisms in perennial plants than in annual plants.

The other recent CG analysis study was performed in an area of 3.7 Mbp in G4 (around the \( Lb \) gene) and showed 429 genes in the peach Lovell genome (Castede et al., 2014). Based on

Table 1 | Identified genes involved in the regulation of flowering time in \( Prunus \) species.

| Specie | Gene   | Gene ID    | Annotation                        | References                  |
|--------|--------|------------|-----------------------------------|-----------------------------|
| P. armeniaca | PHYE   | Q6SCK5     | Phytocrome E                      | GeneBank data               |
| P. armeniaca | RGA    | RGA        | Transcription factor              | Soriano et al., 2005        |
| P. armeniaca | SOC1   | L7Y228     | Transcription factor              | Trainin et al., 2013        |
| P. armeniaca | TFL1   | ADL62862   | Phosphatidylethanolamine binding  | Liang et al., 2010          |
| P. avium | APETALA1 | APETALA1   | MADS-box gene family              | Wang et al., 2013           |
| P. avium | GA1    | GA1        | Gibberellin biosynthesis          | Blake et al., 2000          |
| P. avium | TFL1   | AB636121.1 | Phosphatidylethanolamine binding  | Mimida et al., 2012         |
| P. domestica | FT1    | FT1        | Transcription coactivator         | Tränkner et al., 2010       |
| P. dulcis | GA20   | BU574794   | Gibberellin 20-oxidase            | Silva et al., 2005          |
| P. dulcis | LFY    | PrdLFY     | AFL2                              | Silva et al., 2005          |
| P. dulcis | MADS1  | PrdMADS1   | MdMADS10                          | Silva et al., 2005          |
| P. dulcis | PHYA   | Q94EK7     | Phytochrome A                     | GeneBank data               |
| P. mume | AGL 24 | AB437345.1 | dormancy-associated MADS-box      | Yamane et al., 2008         |
| P. mume | FT     | AM943979   | MADS-box T protein                | Silva et al., 2005          |
| P. serotina | AGAMOUS | EU938640   | Formation of stamens and carpels   | Liu et al., 2010            |
| P. persica | AGL 2  | BU048398   | MdMADS 8                          | Silva et al., 2005          |
| P. persica | AP1    | BU039475   | MdMADS 2                          | Silva et al., 2005          |
| P. persica | AP2    | BU046298   | AHAP2                             | Silva et al., 2005          |
| P. persica | ATM YB33 | XM_007218900 | myb domain protein 33             | Zhu et al., 2012            |
| P. persica | CDF1   | XM_007215192 | cycling DOF factor 2             | GeneBank data               |
| P. persica | CO     | BU042239   | Constans like protein             | Silva et al., 2005          |
| P. persica | DAM 5  | AB932551   | MADS-box 5                        | Yamane et al., 2011         |
| P. persica | DAM 6  | DQ863252   | MADS-box 6                        | Bielenberg et al., 2008     |
| P. persica | FAR 1  | BU047045   | Far-red-impared responsive protein| Silva et al., 2005          |
| P. persica | FPF 1  | XM_007225892 | Flowering promoting factor        | Romeu et al., 2014          |
| P. persica | FRL 1  | DY640223.1 | FRI-related gene                  | Silva et al., 2005          |
| P. persica | FT     | G3GAW0     | Flowering locus T protein         | Silva et al., 2005          |
| P. persica | FT     | BU044758   | Flowering locus T protein         | An et al., 2012             |
| P. persica | LEAFY  | EF175869   | Activator of AP1                  | GeneBank data               |
| P. persica | PHYA   | Q945F7     | Phytochrome A                     | Silva et al., 2005          |
| P. persica | PHYB   | Q945T4     | Phytochrome B                     | GeneBank data               |
| P. persica | TFL1   | ADL62867   | Phosphatidylethanolamine binding  | Liang et al., 2010          |
FIGURE 1 | Location of QTLs linked to flowering time and chilling and heat requirements in the almond map from the population R1000 × Desmayo Largueta performed by Sánchez-Pérez et al. (2007b, 2012). The closest SSR marker linked to the QTL is marked with bold lettering on this map. The approximately location of the RAPD marker (AG6) (Ballester et al., 2001) and candidate genes (in italics) (Silva et al., 2005) linked to flowering time in other almond populations, are indicated inside the boxes. The integration of this information from different genetic maps has been performed using the centimorgan (cM) distances indicated by the different authors in each linkage group and each map.
predicted function of proteins, they selected nine CGs. One of these, ppa002685m, is an embryonic flower 2 gene involved in the vernalization response and a negative regulator of the flower development through histone methylation. It would be interesting to see the analysis of this gene in varieties with different flowering times in almond.

Recently, Zhebentyayeva et al. (2014) developed a comprehensive program to identify genetic pathways and potential epigenetic mechanisms involved in control of chilling requirement and flowering time in peach. These authors described the TFL1, which regulates the vegetative to reproductive transition, and the PcG (polycomb group) genes, which are involved in the epigenetic regulation of flowering in Arabidopsis. It is worth noting that these authors failed to identify a direct FLC gene ortholog and its regulator FRI, suggesting that control of flowering time in Prunus species has a complex genetic architecture.

The recent release of the complete peach genome sequence (Verde et al., 2013) together with four almond genome sequences (Koepke et al., 2013) and the sweet cherry genome publicly available since 2013 (Carrasco et al., 2013), offer new possibilities for integrating genetic and genomic approaches to find new CGs for flowering time in perennial plants (Martínez-Gómez et al., 2012).

TRANSCRIPTOMIC STUDIES
Almond transcriptomic studies have not been performed to date. The only transcriptomic study performed in other Prunus species has been using flower buds of Japanese apricot (Prunus mume Sieb. et Zucc.) at different dormant stages (Habu et al., 2012). In this species, varying flowering time is caused by irregular bud endodormancy release (Zhuang et al., 2013). The transcriptome analysis of flower buds showed 25 endodormant-specific upregulated unigenes. DAM6 was one of them although, in most of the unigenes, no hit was found. As we have previously mentioned, many of the MADS family genes, such as DAM6, are involved in different steps of flower development including flowering time (Riechmann and Meyerowitz, 1997). At this moment, more than 50 MADS-Type Transcription Factors (TFs) have been identified in the peach genome, so further studies should be done to identify more gene products involved in flowering.

In Arabidopsis, flowering time is dependent on intricate genetic networks to perceive and integrate both endogenous and environmental signals (Khan et al., 2014). In the aging pathway, it has been found that the role of five microRNAs (miRNAs) families called miR156, miR172, miR159/319, miR390, and miR399 is important in flowering time (Spanudakis and Jackson, 2014). Recently, miRNAs differently expressed in chilled peach vegetative buds have been identified co-localizing with known QTLs for chilling requirement and flowering time traits (Barakat et al., 2012; Rios et al., 2014). A cascade of miRNAs such as miR156, miR172 and their respective targets SQUAMOSA PROMOTER BINDING PROTEIN-LIKE, and AP2 like genes are involved in modulating flowering induction in Arabidopsis through FT and other flowering related genes (Khan et al., 2014; Spanudakis and Jackson, 2014). Transcriptomic studies in poplar and leafy spurge have shown a differential expression of SPL genes and miR172 during dormancy induction, suggesting that this miRNA pathway may also play a regulating role in dormancy processes that affect flowering time (Rios et al., 2014).

Application of new high-throughput RNA sequencing (RNA-seq) technologies (Flintoft, 2008; Martínez-Gómez et al., 2011) could greatly clarify the TFs involved in the regulation of flowering time, allowing the determination of transcripts from a particular region of the genome.

METABOLOMIC STUDIES
The common by-product upon degradation of hydrogen cyanamide and cyanogenic glucosides is cyanide, which is not only involved in bringing forward flowering time but also in breaking seed dormancy by inducing formation of Reactive Oxygen Species (ROS). ROS activates a cascade in which ETHYLENE RESPONSE FACTOR 1 is implicated, producing germination-associated proteins (Oracz et al., 2007). CBF proteins belong to the CBF/DRE binding sub-family of the APETALA2-ETHYLENE responsive factor (Nakano et al., 2006). The action mechanism of nitrogen-based chemical treatments could involve the regulation of the effect of these TFs.

Further, in stone-fruit species (e.g., Prunus species), the presence of common regulatory mechanisms between the chilling requirements for seed and bud dormancy release have been suggested (Leída et al., 2012). Moreover, secondary metabolites as cyanogens were suggested to be involved in the germination of cocklebur seeds (Xanthium pennsylvanicum Wallr.) in response to various nitrogenous compounds (Esashi et al., 1996). Other cyanogens such as the CNGlc prunasin have been described in flower parts in eucalyptus (Eucalyptus cladocalyx F. Muell.), seeing that young flower buds were the most cyanogenic, when reproductive organs were analyzed at various stages of development (Gleadow and Woodrow, 2000).

The integrated analysis of these well-known mechanisms reveals accumulation of cyanogenic glucosides and regulation of flowering time through TFs, which open new possibilities in the analysis of this complex trait in almond and the rest of Prunus.

NEW PERSPECTIVES
Almond is not only the earliest fruit tree to break dormancy but also shows the widest range of flowering time among all fruit and nut species (Socias i Company and Felipe, 1992), making it a suitable candidate for studying this important trait within perennial plants. There are many genes that are conserved during the evolution of flowering plants. However, there are other mechanisms i.e., miRNAs regulation or metabolite signaling, which could be also included in new studies to deepen the analysis of gene regulation of the flowering time in almond. The final objective continues to be the development of efficient molecular markers for selection in breeding programs. This would enable breeders to select the late flowering individuals in the nursery which would allow them to avoid yield losses due to frosts, which currently occurs in early flowering genotypes.

AUTHOR CONTRIBUTIONS
Raquel Sánchez-Pérez and Pedro Martínez-Gómez participated in the coordination of the study. Federico Dicenta and Jorge Del Cueto collected and revised the genetic information. Pedro Martínez-Gómez and Raquel Sánchez-Pérez collected and revised genomic and transcriptomic information. Raquel Sánchez-Pérez and Jorge Del Cueto collected metabolomics information.
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