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Research review paper

Can a late bloomer become an early bird? Tools for flowering time adjustment

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ABSTRACT

The transition from the vegetative to reproductive stage followed by inflorescence is a critical step in plant life; therefore, studies of the genes that influence flowering time have always been of great interest to scientists. Flowering is a process controlled by many genes interacting mutually in a genetic network, and several hypothesis and models of flowering have been suggested so far. Plants in temperate climatic conditions must respond mainly to changes in the day length (photoperiod) and unfavourable winter temperatures. To avoid flowering before winter, some plants exploit a specific mechanism called vernalization. This review summarises current achievements in the study of genes controlling flowering in the dicot model species thale cress (*Arabidopsis thaliana*), as well as in monocot model species rice (*Oryza sativa*) and temperate cereals such as barley (*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.). The control of flowering in crops is an attractive target for modern plant breeding efforts aiming to prepare locally well-adapted cultivars. The recent progress in genomics revealed the importance of minor-effect genes (QTLs) and natural allelic variation of genes for fine-tuning flowering and better cultivar adaptation. We briefly describe the up-to-date technologies and approaches that scientists may employ and we also indicate how these modern biotechnological tools and “-omics” can expand our knowledge of flowering in agronomically important crops.

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Motto:

“How can we control flowering time?”

“The triggering of flowering is a highly regulated process and, depending on the plant, is influenced by many interacting pathways and environmental influences (light, temperature and so on). Extensive research has revealed many of the mechanisms that control this, especially in the model plant *Arabidopsis*. An even more complete understanding of the processes is needed in major cultivated species, where the ability to fine-tune flowering to the growing season could give significant advantages for both breeders (easier production of hybrids, and faster breeding cycles) and producers (timing of flowering better adapted to specific environments).” (from “One hundred important questions facing plant science research”, (Grierson et al., 2011)).

1. Introduction

Anthesis is the most crucial act that flowering plants undergo to succeed in reproduction and survival over many generations. As a plant cannot move from its position, it should absorb all environmental cues and, at the correct time, make the final decision about its reproduction. This key process is precisely controlled and is continuously and flexibly modified to finish the reproduction cycle at a favourable time. Plants must consider many environmental signals (e.g., day length, temperature, and seasonality) and internal inputs (e.g., length of the juvenile phase and available energy). The understanding of floral development and crucial developmental switch from the vegetative to reproductive phase has been deeply studied in *Arabidopsis thaliana*. At the outset, nearly 70 years ago, researchers presumed the existence of flower-forming substances in the leaves that are essential for forming the floral organ identities. Chailakhyan (Chailakhyan, 1936) introduced the term “florigen” (flower-former) for this floral stimulus. This early work was expanded by many plant biologists for decades and has led to the identification of the genetic background of flowering, key transcription factors and regulatory proteins. Current knowledge about biochemical pathways leading to flowering includes protein–protein interactions and regulatory networks that integrate environmental and internal signals to coordinate the reproductive process in the complex plant organism. Recently, several review articles were published summarising the knowledge of the molecular mechanisms of flowering in *Arabidopsis* (Andrés and Coupland, 2012; Jung and Müller, 2009; Kaufmann et al., 2010; Samach, 2012). The process of flowering and its timing has an indisputably large impact on grain yield in crop species. Unfortunately, the current knowledge of flowering genes and pathways in cereals and other crops is limited to some extent. Comparative and functional genomics revealed some genes orthologous to those previously characterised in *Arabidopsis* with conserved functions. Other flowering time genes found in *Arabidopsis* have distinctive functions in cereals. Some genes influencing flowering time in cereals were not found in *Arabidopsis* (Andrés and Coupland, 2012; Higgins et al., 2010) proposing that vernalization requirement has evolved independently in dicots (*Arabidopsis*) and monocots (cereals) (Jung and Müller, 2009). Recent progress in identifying unique flowering pathways in rice (Tsuji et al., 2011) has confirmed the requirement for a deep understanding of the flowering process in temperate cereals.

As the world's population is supposed to reach 9 billion by 2050, humankind will clearly need more food. Currently, the main cereals (rice, wheat and maize) constitute more than 50% of the total crop production worldwide (<http://www.fao.org/>), and cereal seeds are one of the most important renewable resources of food, feed and industrial raw materials. Crop species of the Triticeae tribe, which comprises wheat, barley and rye, are essential components of human and domestic animal nutrition. It is worth mentioning that their domestication in the Fertile Crescent 10,000 years ago participated in the beginning of agriculture

and contributed to the advancement of civilisation. With 17% of all crop areas, wheat is the staple food for 40% of the world's population, whereas barley ranks fifth in production. Unambiguously, cereals will play a crucial role in food security during the next decades. Among them, wheat has a great potential to increase its yield, which is currently the lowest compared with maize and rice. We definitely must explore all possibilities to increase the production of cereals, including fine-tuning the flowering time to local conditions to fulfil the growing demands for food. There is strong evidence that genes controlling flowering affect both mass and grain production and are thus likely to impact the yield (Jung and Müller, 2009; Ni et al., 2009). A comprehensive understanding of flowering regimes in cereals and mining new alleles are major goals for crop improvement and plant breeding efforts to produce novel cultivars, which will be better adapted to local environments and changing climatic conditions.

Herein, we will review the key mechanisms controlling flowering in *Arabidopsis*, rice and temperate cereals. Furthermore, recent advances in genomics and biotechnology with a focus on flowering time manipulation in temperate cereals will be discussed.

2. Photoperiod response

Plants respond to changes in the day length (photoperiod) during the year by precisely controlled mechanisms, which affect the timing of flowering and reproduction. With respect to the photoperiod required for flowering, plants can be classified as long-day (flowers under long days), short-day (flowers under short days) and day-neutral (insensitive to day length). The main genes involved in the photoperiod pathway of *Arabidopsis*, rice and temperate cereals (wheat and barley) are described below. A comparison of these key genes among individual species is depicted in Fig. 1.

2.1. *A. thaliana*

The transition from the vegetative to reproductive phase and the development of floral organ identities have been intensively studied in the *Arabidopsis*. The perception of photoperiod evidently occurs in the leaves, but the floral organs arise from the shoot apical meristem. Thus, the existence of a moving signal termed “florigen” was suggested in the past (Chailakhyan, 1936). This signal was proved to be at least partially realised by a protein encoded by *FLOWERING LOCUS T (FT)* (reviewed in Turck et al., 2008). FT can be transported from phloem companion cells to the shoot apical meristem through phloem sieve elements, providing the transition of the photoperiod signal to the site of flower formation (Corbesier et al., 2007). Recently, the transport of FT to the sieve elements of the phloem was proved to require a membrane protein called FT-INTERACTING PROTEIN 1 (FTIP1) (Liu et al., 2012a). The activation of FT requires the expression of *CONSTANS (CO)*, which encodes the zinc finger transcription regulator of the FT promoter (Tiwari et al., 2010). The activity of CO is responsive to light and the circadian clock. CO transcription is induced by the interactions of plant-specific protein GIGANTEA (GI), ubiquitin ligase FLAVIN KELCH F BOX 1 (FKF1) and photoreceptors (phytochromes and cryptochromes). These proteins are components of the pathway (s) responsible for the circadian clock in plants (Baudry et al., 2010; De Montaigu et al., 2010). Under long days, the light-dependent interaction between GI and FKF1 releases the repression of CO by inducing the degradation of the transcription repressor known as CYCLING DOF FACTORS (CDFs) (Sawa et al., 2007). The photoperiodic control of flowering through CO/FT and homologous genes is widely conserved among long-day plant species (Turck et al., 2008).

After the transfer to the shoot apical meristem, FT interacts with the bZIP transcription factor *FLOWERING LOCUS D (FD)* (Corbesier et al., 2007). This protein–protein complex (FT–FD) activates the expression of the *SQUAMOSA BINDING PROTEIN LIKE (SPL)* genes that encode a family of transcription factors, which play a conserved central role in the floral

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