

# Age-dependent and winter temperature pathways regulate flowering in perennial plants

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Flowering time plays significant role for the reproductive success of plants. If flowering is initiated at the wrong time, it will affect the number of seeds produced and significantly reduce reproductive success. Arabidopsis, as the premier model system for molecular and genetic analyses of plant development, has provided a substantial insight into important pathways and mechanisms of its architecture. Four major pathways to flowering have been characterized in Arabidopsis; including environmental induction through photoperiod, temperature, autonomous floral initiation, and regulation by gibberellins [1]. Now a new pathway has been added to these known genetic pathways: age pathway [2]. Recently, targets of two age-regulated miRNAs (miR156 and miR172) have been implicated in the timely control of several phase transitions in various plant species [2-4].

MiR156 is highly abundant in juvenile stage, and decreases during subsequent adult stage, while miR172 has an opposite expression pattern [2,4], thereby suggesting a complementary regulatory relationship between miR156 and miR172. Over-expression of miR156 negatively regulates several SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (SPL) genes, and delays both the juvenile-to-adult and adult-to-reproductive phase transitions. However, miR156/172 are often excluded from these models, because their extreme genetic redundancy, as well as the complexity of their regulation by miRNAs have made it difficult to pinpoint their exact functions in development [4]. Interestingly, more and more studies indicate that the age pathway play an important role in regulating flowering of annual and perennial plants.

The progress in understanding the flowering process in model plant systems has given us an insight into the molecular events responsible for transition from vegetative to reproductive phase in other plants. Perennials undergo transitions are also triggered during their life cycle by some external and endogenous factors [1]. Therefore, most of the current molecular knowledge on the flowering process has been obtained from the model plant system because of a variety of technical limitations associated with perennial plants, usually related to their size, long generation times, as well as limited genetic knowledge [5]. For perennial plants, flowering occurs only in the adult phase [1,6] and is restricted to a subset of axillary meristems compare with annual plants to ensure continuation of vegetative growth [5]. Another trait vital to survival is the capacity of meristems to transit into a dormant and freezing-tolerant state at the end of the growing season [7]. The biology of these seasonal transitions in shoot apical meristem behavior cannot be investigated in Arabidopsis, perhaps explaining why the understanding of their molecular regulation is still limited. Recently, Bergonzi et al. [8] and Zhou et al. [9] studied how molecular signals translate environmental information—such as exposure to a low temperature or changes in day-length and physiological information, such as age of the plant—into signals that promote flowering of perennial plants.

During *Cardamine flexuosa* and *Arabis alpina* flowering regulation process, age and vernalization pathways are integrated through

the regulation of miR156 and miR172. Zhou et al. [9] studied the molecular mechanisms that regulate flowering in the biennial-to-perennial *Cardamine flexuosa* [10]. The results demonstrate that the levels of miR156 and miR172 determine the timing of sensitivity in response to low temperature in *Cardamine flexuosa*. Age and vernalization pathways coordinately regulate flowering through modulating the expression of SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1, a flower-promoting MADS-box gene, and removing two repressors, FLOWERING LOCUS C, which is repressed by vernalization, and TARGET OF EAT1, which is down-regulated by the miR156-SPL-miR172 cascade in *Cardamine flexuosa* [10].

The findings represent the first example of plants using age cues to respond to environmental cues, and thus may have implications for plant evolution. Meanwhile, Bergonzi et al. (2013) used *Arabis alpina* as a model, to study how increasing age and exposure to winter cold coordinate to establish competence to flowering [8,9]. The results also indicate that miR156 levels decline as *Arabis alpina* ages, causing increased production of SPL genes and ensuring that flowering occurs in response to low temperature of winter. On the other hand, the age at which plants respond to vernalization can be altered by manipulating miR156 levels.

Although miR156 and miR172 levels are uncoupled differently in *Arabis alpina* compared with Arabidopsis, miR156 abundance represents the timer controlling age dependent flowering responses to cold. Additionally, the results also show that the AP2 transcription factor (PEP2), a target of miR172, prevents flowering before vernalization [8]. These findings indicate that miR156 and PEP2/PEP1 act in parallel repressive pathways to ensure that *Arabis alpina* meristems become competent to flower only if they have reached the appropriate age and have been exposed to winter temperatures [8].

Taken together, the integration of age and vernalization pathways offers an advantage for the perennial growth habit by ensuring that plants do not flower until they develop axillary vegetative shoots and sufficient biomass.

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