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# The Right Time and Place for Making Flowers

Miguel A. Blázquez

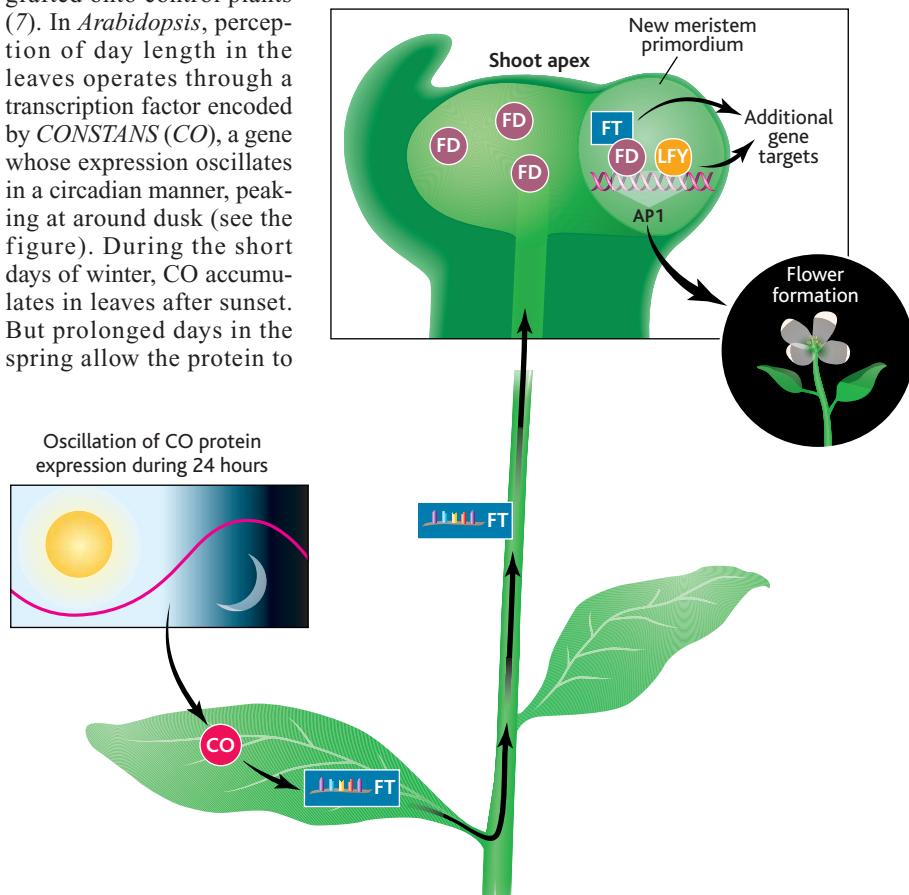
**R**eproductive success in plants depends on the synchronization of flowering within a given species. Many plants have developed a highly complex signaling network that monitors environmental conditions, such as day length, temperature, or nutrient availability, and determines the appropriate timing for flowering (1, 2). This is the case for the model plant *Arabidopsis thaliana* and the pea that both flower in spring when day length and ambient temperature increase, or certain rice varieties and soybean that flower early in the fall when days get shorter. The initiation of flowering requires an additional developmental program to specify the floral identity of the new structures that continuously arise at the shoot apex (3). For instance, during the long vegetative phase in *Arabidopsis*, every primordium, the groups of cells poised to differentiate, forms a leaf. However, once the decision to flower has been made, all newly emerging primordia follow a developmental program that culminates in the formation of flowers rather than leaves. Thus, constructing a flower requires both temporal and spatial information that restricts the initiation of flowering to specific locations. But how this information is integrated has not been clear. Three studies now reveal the molecular mechanism by which this integration is achieved. In this issue, Abe *et al.* on page 1052 (4) and Wigge *et al.* on page 1056 (5) report that interaction between Flowering Locus T (FT), a protein encoded by a gene that is expressed in leaves, and FD, a bZIP transcription factor that is present only in the shoot apex, triggers the expression of floral identity genes in the new primordia. The third paper by Huang *et al.* in this week's *Science Express* (6) reports how the two factors meet—FT transcript travels from leaf to shoot via the plant vascular tissue.

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It has been known for at least 50 years that flowering is triggered at the shoot apex through a mobile signal, or "florigen," that is generated in leaves in response to conditions that promote the production of flowers. In a classic experiment, the leaves of florigen-induced *Perilla crispa* plants promoted flowering when grafted onto control plants (7). In *Arabidopsis*, perception of day length in the leaves operates through a transcription factor encoded by *CONSTANS* (*CO*), a gene whose expression oscillates in a circadian manner, peaking at around dusk (see the figure). During the short days of winter, *CO* accumulates in leaves after sunset. But prolonged days in the spring allow the protein to

## OF OVEREXPRESSION OF CONSTANS

1. Interestingly, *CO* acts in the phloem, the vascular tissue of plants, to activate *FT* expression in leaves in a cell-autonomous manner. This is based on the observation that *CO* activates *FT* expression and promotes flowering only when expressed under the control of phloem-specific promoters in the leaf, but not apex-specific promoters in the shoot (9, 10). These results suggest that the activity of *CO* is central for the generation of the mobile signal that originates in the leaf but has to be perceived in the apex to establish flowering. The up-regulation of *FT* expression by *CO* is required because loss of *FT* function prevents early flowering caused by overexpression of *CO*, whereas



**Integration of signals to generate a flower.** Appropriate day length allows the accumulation of the transcription factor *CO* that controls expression of *FT* in the leaf. (Inset) *FT* transcript moves through the phloem to the shoot apex where the *FT* protein is produced and interacts with the transcription factor *FD*. The complex then activates key genes such as *AP1* to start flower development. *LEAFY* (*LFY*) is a transcription factor required for *AP1* expression in wild-type plants. *LFY* expression is up-regulated by *FT* in the shoot apex.

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accumulate in the presence of light, the stimulus that activates *CO* (8). Over-expression of *CO* causes early flowering, and among the target genes directly activated by *CO*, two seem to be most relevant for floral induction: *FT* and *SUPPRESSOR*

increasing *FT* expression causes premature flowering (11, 12). Thus, an important question has been how *FT* produced in the leaves would activate the transcription of floral identity genes, such as *APETALA1* (*API*), at the shoot apex.

To solve the spatial paradox of FT action, Abe *et al.* and Wigge *et al.* analyzed a gene encoding a new bZIP transcription factor, FD, that is expressed preferentially at the shoot apex in the region where new primordia are being generated (4, 5). Multiple lines of evidence in these studies suggest a model by which FD provides the spatial framework for timely activation of flowering by FT. First, FD is required by FT to promote flowering because mutations in the *FD* gene delayed both up-regulation of *AP1* expression and the early flowering phenotype caused by *FT* overexpression. Second, although *FD* is not as efficient as *FT* in promoting early flowering when either one is overexpressed, there was synergistic interaction between them in plants that overexpress both factors. And third, FT and FD proteins interact physically, as shown in yeast by two-hybrid assays and as seen in plants by fluorescence microscopy.

How relevant is the interaction between FT and FD for the regulation of flowering? FT has no known DNA binding domain. However, constitutive expression of a fusion protein containing FT and the glucocorticoid receptor accelerated flowering in the presence of dexamethasone, a synthetic steroid that activates the glucocorticoid receptor and allows translocation of the fusion protein into the nucleus (4). Furthermore, a key experiment strongly suggests that FD and FT act together to activate downstream targets: Ectopic expression of FD caused up-regulation of *AP1* expression in leaves only when they were subjected to treatments that increase *FT* expression, such as transfer of plants from short- to long-day conditions (5).

The finding that FT and FD act together to activate reproductive development in plants fills a gap in our understanding of how temporal information and spatial constraints are integrated, but several questions remain. For instance, it is intriguing how *AP1* expression is established precisely in floral primordia, given that *FD* is more widely expressed in the shoot apex. As proposed by Abe *et al.*, other proteins must restrict *AP1* expression to the correct location, and in this context, it is worth mentioning that TERMINAL FLOWER 1, a protein with strong sequence similarity to FT, is a well-known regulator of *AP1* expression that prevents AP1 from invading the central part of the shoot apex (13).

The model presented by Abe *et al.* and Wigge *et al.* implies that FT itself might be an important component of the elusive mobile signal that induces flowering, because *FT* is expressed in a plant tissue

different from the cells in which its direct interaction with FD is needed. The study by Huang *et al.* (6) answers this question, showing that the transcript of *FT* moves from the leaf to the shoot apex. By locally inducing *FT* expression in a single *Arabidopsis* leaf, the authors demonstrate that a pulse of *FT* expression in the leaf results in transport of the *FT* transcript to the shoot apex, and is sufficient to trigger flowering. Indeed, long-distance movement of RNAs through the phloem has been well documented in plants (14), but it remains to be determined if specific proteins are involved in the transport of *FT* transcripts through the phloem. In a more complicated scenario, *FT* presence in the apex might also be the result of the activity of a different *FT*-induced signal moving through the phloem or from cell to cell. Movement of transcription factors through plasmodesmata, junctions that allow direct communication between the cytoplasm of adjacent plant cells, has also been described (15). It remains to be determined if specific

proteins are involved in the transport of *FT* transcripts through the phloem. Although the composition of the florigenic signal is very likely complex (16), it seems that our understanding of this phenomenon is coming full circle.

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## GEOCHEMISTRY

# Biogeochemical Cycling of Iron Isotopes

Clark M. Johnson and Brian L. Beard

**I**ron is the most abundant element that engages in reduction-oxidation (redox) chemistry. The ferrous form ( $\text{Fe}^{2+}$ ) is dominant in the core, mantle, and deep crust, but ferric iron ( $\text{Fe}^{3+}$ ) is stable under current atmospheric conditions and hence is the stable oxidation state in most surface environments. At the same time, some of the largest fractionations in the isotopic composition of iron {commonly expressed as  $\delta^{56}\text{Fe} = [({^{56}\text{Fe}}/{^{54}\text{Fe}}_{\text{Sample}})/({^{56}\text{Fe}}/{^{54}\text{Fe}}_{\text{Standard}}) - 1] \times 10^3$ } occur between oxidized and reduced forms. Because biochemistry involves changes in redox state, this fractionation process has been a major motivation for developing this isotopic system as a means for tracing biogeochemical phenomena. In environments that contain iron in both oxidation states, the oxidized form is generally enriched in the heavy isotopes on the order of several per mil (parts per thousand, or ‰) at room temperature. This behavior is seen across all of the transition elements that have multiple oxidation states (1). In terms of isotopic studies of the transition elements, iron

has received the most attention because of its high abundance on Earth and its prominent role in biogeochemical processes.

More than 60 papers have been published on iron isotope geochemistry since the field initially gained visibility in 1999, and these works have addressed issues ranging from biological processing of iron (2) to the rise of oxygen in the atmosphere (3). Collectively, studies of natural samples, as well as the critical laboratory-determined equilibrium and kinetic isotope fractionation factors in abiotic and biotic systems, have provided an initial picture of isotopic variations that are produced by global biogeochemical cycling of iron (see the figure). A remarkably large portion of the iron inventory on Earth is isotopically homogeneous ( $\delta^{56}\text{Fe} = 0\%$  relative to an igneous rock standard), including igneous rocks and sedimentary rocks that have undergone minimal chemical change after deposition (4). Although iron-isotope variations within the mantle could arise as a result of high-pressure mineral fractionation and/or chemical changes, these variations are apparently homogenized during magma generation,

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