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 *Arabidposis* 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 invloved 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.

References

1. M. J. Yanovsky, S. A. Kay, *Nat. Rev. Mol. Cell Biol.* **4**, 265 (2003).
2. G. G. Simpson, C. Dean, *Science* **296**, 285 (2002).
3. Y. Komeda, *Annu. Rev. Plant Biol.* **55**, 521 (2004).
4. M. Abe *et al*., *Science* **309**, 1052 (2005).
5. P. A. Wigge *et al*., *Science* **309**, 1056 (2005).
6. T. Huang *et al*., *Science* 11 August 2005 (10.1126/science.1117768).
7. J. A. D. Zeevaart. *Annu. Rev. Plant Physiol.* **27**, 321 (1976).
8. F. Valverde *et al*., *Science* **303**, 1003 (2004).
9. H. An *et al*., *Development* **131**, 3615 (2004).
10. B. G. Ayre, R. Turgeon, *Plant Physiol.* **135**, 2271 (2004).
11. Y. Kobayashi *et al*., *Science* **286**, 1960 (1999).
12. I. Kardailsky *et al*., *Science* **286**, 1962 (1999).
13. O. J. Ratcliffe *et al*., *Development* **126**, 1109 (1999).
14. S. Ueki, V. Citovsky, *BioEssays* **23**, 1087 (2001).
15. A. Sessions, M. F. Yanofsky, D. Weigel, *Science* **289**, 779 (2000).
16. G. Bernier *et al*., *Plant Cell* **5**, 1147 (1993).

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GEOCHEMISTRY

Biogeochemical Cycling of Iron Isotopes

Clark M. Johnson and Brian L. Beard

Iron is the most abundant element that engages in reduction-oxidation (redox) chemistry. The ferrous form (Fe^{2+}) is dominant in the core, mantle, and deep crust, but ferric iron (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 $\delta^{56}\mathrm{Fe} = [(^{56}\mathrm{Fe}/^{54}\mathrm{Fe}_{\mathrm{Sample}})/(^{56}\mathrm{Fe}/^{54}\mathrm{Fe}_{\mathrm{Standard}}) - 1] \times 10^3$} 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 abiologic and biologic 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 (δ^{56}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,

The authors are in the Department of Geology and Geophysics, University of Wisconsin–Madison, Madison, WI 53706, USA. E-mail: clarkj@geology.wisc.edu