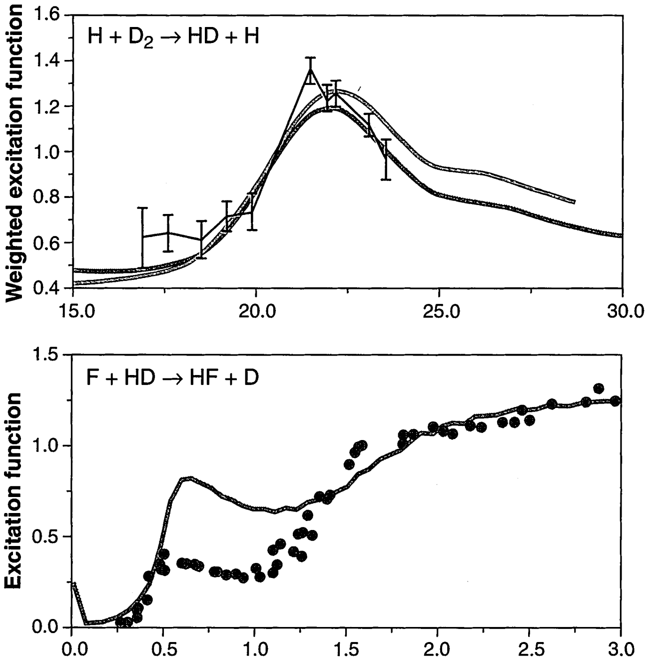
measurable properties are determined either by experiment or simulation. As a result, past studies of H + H_2, F + H_2, and similar reactions have been unable to attribute observed features to resonances with certainty.



Now you see it. Excitation function (cross section versus translational energy) for H + D_2 [top panel, based on data from (*1*)] and F + HD [bottom panel, based on data from (*2*)]. Each plot presents the measured results (data points in red) and the results of theoretical simulations (blue and/or green curves). The peak seen in each panel is a characteristic signature of resonance behavior. In the case of H + D_2, the measured results involve an average over scattering angles that depends on experimental parameters. This results in two slightly different theoretical estimates (blue and green curves), depending on the estimated uncertainty.

One way to circumvent the averaging problem is to perform a direct spectroscopic measurement of the transition state for the chemical reaction. Such measurements were pioneered by Neumark and coworkers in 1990 (*11*), who used photodetachment spectroscopy on the anion precursor to the neutral transition state. With this technique, resonances were seen in the transition state of the I + HI reaction. But the corresponding measurements for F + H_2 were dominated by other dynamical features (*12*), and no definitive assignment of resonances could be made.

The new reports of resonances in H + D_2 and F + HD are based on measurements under circumstances where resonance behavior is not canceled out by collisional averaging. The studies of F + HD reported by Skodje *et al.* (*2*) involve crossed molecular beam measurements at low collision energies, with simultaneous measurements of the angular and translational energy distributions of the products. The H + D_2 laser photolysis work by Kendrick *et al.* (*1*) involves simultaneous measurements of product translational and rotational energies. In both studies, a peak in the energy dependence of the cross sections is observed, which is characteristic of resonance behavior (see figure on the left). The resonance in H + D_2 has a very short lifetime (~10 femtoseconds), whereas that in F + HD is longer lived (~100 femtoseconds). The very short lifetime in H + D_2 barely allows the HD_2 intermediate to oscillate twice. The longer lifetime of the FHD intermediate corresponds to tens of vibrational periods. The key factor stabilizing this resonance is the low mass of H relative to F and D.

The new measurements provide unique information about transition state properties that will be important to understanding properties of potential energy surfaces. In addition, the observations should pave the way for more routine observations of reactive resonances in the future.

References and Notes

1. B. K. Kendrick, L. Jayasinghe, S. Moser, M. Auzinsh, N. Shafer-Ray, *Phys. Rev. Lett.* **84**, 4325 (2000).
2. R. T. Skodje *et al.*, *J. Chem. Phys.* **112**, 4536 (2000).
3. G. C. Schatz and A. Kuppermann, *J. Chem. Phys.* **59**, 964 (1973).
4. R. D. Levine and S.-F. Wu, *Chem. Phys. Lett.* **11**, 557 (1971).
5. D. M. Neumark *et al.*, *J. Chem. Phys.* **82**, 3067 (1985).
6. F. J. Aoiz, V. Herrero, V. Saez Rabanos, *J. Chem. Phys.* **97**, 7423 (1992).
7. F. J. Aoiz, V. Herrero, M. Noqueira, V. Saez Rabanos, *Chem. Phys. Lett.* **204**, 259 (1993).
8. E. Wrede and L. Schnieder, *J. Chem. Phys.* **107**, 786 (1997).
9. F. London, *Z. Elektrochem.* **35**, 532 (1929).
10. H. Eyring and M. Polanyi, *Z. Phys. Chem.* **B12**, 279 (1931).
11. I. M. Waller, T. Kitsopoulos, D. M. Neumark, *J. Phys. Chem.* **94**, 2240 (1990).
12. D. E. Manolopoulos *et al.*, *Science* **262**, 1852 (1993).
13. I acknowledge support from NSF grant CHE-9873892.

PERSPECTIVES: PLANT BIOLOGY

Flower Arranging in *Arabidopsis*

Paul F. Devlin and Steve A. Kay

One of the key factors contributing to the success of flowering plants is their ability to regulate the timing of flowering so that they can take maximum advantage of the most environmentally favorable conditions. Unraveling the signal transduction pathways that regulate flowering is one of the most exciting areas of plant biology research. Now, Samach *et al.* (*1*) on page 1613 of this issue and Blázquez and Weigel (*2*) in a recent issue of *Nature* reveal the integrated network of molecular signals that induce flowering in the weed *Arabidopsis thaliana* under different environmental conditions.

Many plants show a strong seasonality in their flowering, which ensures that their seeds are produced when conditions are optimal for germination and growth. Plants are able to accurately measure day length by integrating signals from photoreceptors and an endogenous circadian clock. In long-day species such as winter wheat (*Triticum aestivum*), flowering is induced when the duration of light exceeds a certain critical length. In contrast, short-day plants such as soybean (*Glycine max*) measure the dark period and flower when the night exceeds a certain critical length (*3*). Many plants also flower in response to cold temperatures (vernalization), mimicking the transition from winter to spring when conditions for seed germination are more favorable (*4*). Flowering can also be triggered by environmental stresses such as shading by neighboring vegetation. In this case, plant species can best succeed by channeling all of their available energy into reproduction (*5*).

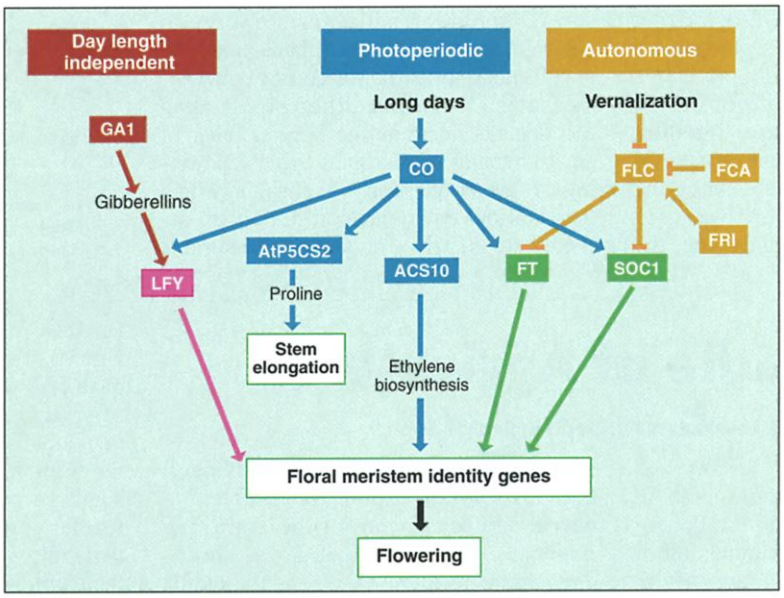
Arabidopsis is a facultative long-day plant, that is, it flowers vigorously during long days (it also flowers in response to cold). These flowering responses are regulated by the photoperiodic and autonomous signaling pathways (see the figure). However, in the absence of promoting signals, *Arabidopsis* eventually flowers through a day length–independent pathway that follows an age-dependent developmental program (*6*). The study of *Arabidopsis* flowering mutants reveals much about the signal-

---

The authors are in the Department of Cell Biology and National Science Foundation for Biological Timing, Scripps Research Institute, 10550 North Torrey Pines Road, La Jolla, CA 92037, USA. E-mail: pdevlin@scripps.edu, stevek@scripps.edu

ing pathways that regulate each of the flowering responses (*6*). *Embryonic flower* mutants have demonstrated that flowering is, in fact, the default state and that the autonomous pathway normally suppresses the transition from the vegetative to the flowering state. Variations in flowering between different *Arabidopsis* populations have led to the identification of the *FLOWERING LOCUS C* gene (*FLC*), a crucial component of the autonomous pathway. The vernalization response in *Arabidopsis* suppresses the *FLC* gene, thereby negating the autonomous suppression of flowering (see the figure). Conversely, the photoperiodic pathway and the day length–independent (age-dependent) pathway appear to act independently of the autonomous pathway to promote the transition to flowering.

A number of day length–insensitive mutants, including *constans* (*co*) and *flowering locus t* (*ft*), result in the suppression of flowering normally induced by long days. The *co* and *ft* mutants fail to show promotion of flowering during long days, resulting in the assignment of CO and FT to the photoperiodic pathway (see the figure). Finally, mutants such as *ga1* (deficient in the phytohormone gibberellin) demonstrate that gibberellins (in the absence of other promoting signals) are required for flowering that is independent of day length (see the figure).



Flower power. Integration of the signaling pathways that promote flowering in *Arabidopsis*. In response to long days, the photoperiodic pathway (blue) induces expression of the *CONSTANS* gene (*CO*). The transcription factor encoded by *CO* induces expression of four target genes. These are *AtP5CS2*, which promotes stem elongation mediated by proline; *ACS10*, which is thought to promote flowering mediated by ethylene; and *FT* and *SOC1*, two genes previously shown to promote flowering in response to long days. The *FCA* gene is required for full induction of *SOC1* and *FT* by *CO*. It forms part of the autonomous pathway (yellow) regulating the floral suppressor *FLC*. Both the photoperiodic and autonomous pathways converge on the promoters of the *FT* and *SOC1* genes (green). The floral meristem identity gene, *LFY*, is indirectly regulated by *CO* and by the phytohormone, gibberellin, which is a component of the day length–independent pathway (red). Through distinct cis elements, these two pathways converge on and interact with the *LFY* promoter (magenta).

Samach and colleagues investigated the integration of signals from the photoperiodic (day length–dependent) and autonomous pathways. They examined the action of CO in the photoperiodic pathway and observed increases in *CO* messenger RNA in response to long days (*6*). The *CO* gene encodes a GATA-type transcription factor (*7*), suggesting that an increase in CO protein promotes the switching on of other genes in the flowering pathway. To analyze CO-activated genes, the investigators engineered plants to express a fusion protein composed of CO and the ligand-binding domain of the glucocorticoid receptor. The glucocorticoid receptor fusion protein resides in plant cell cytoplasm and is rendered inactive by chaperone proteins. Treatment with the steroid dexamethasone causes the chaperones to release the fusion protein, which then moves to the nucleus and activates the transcription of genes downstream of *CO* in the flowering pathway. By combining the fusion protein approach with the application of the protein synthesis inhibitor cycloheximide, Samach and co-workers were able to identify four target genes that are switched on by CO. They are *FT* and *SUPPRESSOR OF OVEREXPRESSION OF CO 1* (*SOC1*)—already known to be necessary for CO to promote flowering (*6*)—and *AtP5CS2* and *ACS10*, which are involved in shoot elongation and ethylene biosynthesis, respectively (see the figure).

Within the autonomous pathway, FCA suppresses the expression of the *FLC* gene. Consequently, *fca* mutants are constitutively late flowering; that is, flowering is delayed relative to wild-type plants under all conditions (*6*). By analyzing the effect of the *fca* mutation on the ability of CO to induce gene expression, the authors were able to deduce that transcription of *FT* and *SOC1* is also under the control of the autonomous pathway. They demonstrated that FCA is required for full induction of *FT* and *SOC1* by CO. These findings highlight the integration of signals from the autonomous and photoperiodic pathways that together directly control expression of *FT* and *SOC1*. The balance between regulation by the autonomous and photoperiodic pathways differs for *SOC1* and *FT*. Consistent with this, *soc1* mutants flower late under the influence of both long and short days, whereas *ft* mutants flower late in response to long days only. Vernalization also suppresses *FLC*, and so, according to this model, *SOC1* and *FT* are common components of pathways regulating flowering in response to different environmental signals.

In a complementary study, Blázquez and Weigel (*2*) investigate the integration of flowering signals from the photoperiodic and day length–independent pathways. The induction of flowering ultimately leads to the expression of meristem identity genes, consistent with the transition of the meristem from a vegetative state (when it only produces leaves) to a floral state (*8*). (The apical meristem is the active growing point of the plant producing cells destined to become leaves, stem, and flowers.) The authors generated a reporter construct by fusing the promoter of one meristem identity gene, *LEAFY* (*LFY*), to β-glucuronidase (a bacterial gene that produces a colored product when incubated with a substrate). They were able to demonstrate convergence of the photoperiodic and day length–independent pathways (see the figure). The expression of *LFY* is induced, albeit indirectly, by *CO* through the photoperiodic pathway (*1*, *2*) and by gibberellins through the day length–independent pathway (*2*). Until now, it has been unclear whether these pathways converged at *LFY* or at a point upstream of *LFY*.

The authors found that gibberellins activated the *LFY* promoter through cis-acting elements that differed from those inducing the day length flowering response. They generated deletion mutations in the *LFY* gene promoter of the reporter construct and engineered plants to express the mutant constructs. Disruption of a region of the *LFY* promoter containing a consensus sequence for binding of MYB transcription factors resulted in abrogation of the gibberellin response, which is essential for promotion of flowering in *Arabidopsis* during noninductive short days.

The investigators observed normal flowering in response to long days with the mutant constructs. When *CO* was overexpressed, constitutively activating the photoperiodic pathway, reporter gene expression in the mutant construct was also constitutively activated. However, when *FT* was overexpressed, activating the photoperiodic pathway, reporter gene expression was silent, indicating that *LFY* acts downstream of *CO* but not of *FT*. Therefore, *LFY* must be in a signaling pathway that is parallel to that containing *FT* (see the figure). Similarly, when the same disrupted promoter region was used to drive expression of the *LFY* gene, the construct was able to rescue flowering in plants deficient in *LFY* during long days but not short days. This confirms that the disruption constitutes a short-day defect. The *LFY* promoter thus defines another site where different environmental stimuli that control flowering converge and are integrated.

The integration of diverse stimuli in the control of a response is a feature of many biological systems. The two new studies provide inroads into understanding how several signaling pathways converge to control flowering in higher plants, but there is still much to learn. We do not know the mechanism by which different signaling components integrate the large number of environmental stimuli that regulate flowering. A further question is the way in which these various environmental stimuli are detected. It is still a mystery how signals from photoreceptors and the endogenous circadian clock interact to enable plants to detect day length (*9*) or how cold temperatures are sensed, triggering the vernalization response (*10*).

References

1. A. Samach *et al., Science* **288**, 1613 (2000).
2. M. A. Blázquez and D. Weigel, *Nature* **404**, 889 (2000).
3. B. Thomas and D. Vince-Prue, *Photoperiodism in Plants* (Academic Press, London, 1997).
4. K. Napp-Zinn, *Manipulation of Flowering*, J. G. Atherton, Ed. (Butterworths, London, 1987), p. 123.
5. H. Smith, *Photomorphogenesis in Plants*, R. E. Kendrick and G. H. M. Kronenberg, Eds. (Kluwer, Dordrecht, Netherlands, ed. 2, 1994), p. 377.
6. G. G. Simpson, A. R. Gendall, C. Dean, *Annu. Rev. Cell Dev. Biol.* **15**, 519 (1999).
7. J. Putterill, F. Robson, K. Lee, R. Simon, G. Coupland, *Cell* **80**, 847 (1995).
8. M. F. Yanofsky, *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **46**, 167 (1995).
9. D. E. Somers, P. F. Devlin, S. A. Kay, *Science* **282**, 1488 (1998).
10. J. Chandler, A. Wilson, C. Dean, *Plant J.* **10**, 637 (1996).

PERSPECTIVES: ARCHAEOLOGY

The Cradle of Agriculture

Simcha Lev-Yadun, Avi Gopher, Shahal Abbo

A crucial event in human history was the beginning of agriculture about 10,000 years ago in the Pre-Pottery Neolithic Near East. The accumulation of surplus food supplies enabled large settlements to be established, resulting in the emergence of Western civilization. There has been much debate about exactly when and where agriculture first began. Kislev (*1*) proposed that cereals were domesticated after 7000 B.C., later than previously assumed (noncalibrated ^{14}C dates). In contrast, Hillman and Colledge (*2*) recently suggested that rye and pulses were first domesticated during the late Epipaleolithic at Tel Abu Hureyra 1, 8900 to 8600 B.C. If confirmed, these would be the earliest domesticated crops reported.

Enhanced online at www.sciencemag.org/cgi/content/full/288/5471/1602

Regarding the "where" question, it is generally believed that plant domestication first took place in the Jordan Valley and adjacent areas of the southern Levant (in present-day Israel and Jordan). However, we think that botanical, genetic, and archaeological evidence point to a small core area within the Fertile Crescent—near the upper reaches of the Tigris and Euphrates rivers in present-day southeastern Turkey/northern Syria—as the cradle of agriculture (see the figure).

The wild progenitors of all seven Neolithic founder crops (einkorn wheat, emmer wheat, barley, lentil, pea, bitter vetch, and chickpea) as well as flax are found together only in this core area of the Fertile Crescent (see the figure). Wild chickpea grows only in this restricted core area, and its limited distribution is an important clue to the origins of farming in the Near East (*3*). It is unlikely that such a rare species would have been domesticated as a founder crop 10,000 years ago had farming originated outside of this restricted core area. Furthermore, the putative site of einkorn wheat domestication lies within the limited distribution of wild chickpea (see the figure) (*4*). The archaeological record also provides evidence to support the view that the wealthy, farming-based Neolithic societies of the core area were the earliest settlements of this type in the Fertile Crescent.

Near-Eastern Neolithic agriculture was based on three cereals (einkorn wheat, emmer wheat, and barley), four pulses (lentil, pea, chickpea, and bitter vetch), and a fiber crop (flax). Wild chickpea has been found in only 10 locations within a small area in southeastern Turkey/northern Syria (*3*). The distribution of the wild progenitors of the other crops extends across the Fertile Crescent and beyond (*5*) (see the figure). The genetic founder stocks that gave rise to domesticated einkorn wheat (*4*), pea (*5*), and lentil (*6*) have been traced to a small region in or near the limited range of wild chickpea. The notion of a single core area of plant domestication is further supported by the limited genetic variability of modern crops compared with their wild progenitors (*3*) and by genetic evidence suggesting that these crops were domesticated only once (with the possible exception of barley) (*7*). Given the revolutionary nature of the transition from foraging to farming, it seems unlikely that agriculture was invented independently in several locations within the Fertile Crescent in a short period. Had such a transition taken place at different locations, it should have been possible to trace the original founder stocks to different areas. But this has not been the case.

Remains of wild forms of einkorn and emmer wheat, barley, chickpea, lentil, bitter vetch, flax, and possibly pea have been found in pre-Neolithic sites of the Fertile Crescent core area (*1*, *5*) including Tell Abu Hureyra 1 (the site described by Hillman and Colledge) and Tell Mureybet I and II (9000 to 8000 B.C.). They have also been discovered in Neolithic sites at Jerf el-Ahmar, Mureybet III, Djade, and Cayönü (8000 to 7500 B.C). Wild forms have been unearthed at sites near the core area, such as pre-Neolithic Hallan Çemi Tepesi and Neolithic Qermez Dere and M'lefaat (*8*) (see the figure). Domesticated forms of einkorn wheat, emmer wheat, and barley appeared in core-area Neolithic sites at Tell Abu Hureyra 2A and Cafer Hüyük about 7500 B.C., and soon thereafter at Cayönü and Nevali Çori (*1*, *9*).

S. Lev-Yadun is in the Department of Agronomy and Natural Resources, Agricultural Research Organization, Volcani Center, 50250 Bet Dagan, Israel. E-mail: vcfield@agri.gov.il. A Gopher is at the Sonia and Marco Nadler Institute of Archaeology, Tel Aviv University, 69978 Tel Aviv, Israel. E-mail: agopher@post.tau.ac.il S. Abbo is in the Department of Field Crops, Faculty of Agricultural, Food and Environmental Quality Sciences, Hebrew University of Jerusalem, 76100 Rehovot, Israel. E-mail: abbo@agri.huji.ac.il