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stantial influx of data, the differences may be resolved soon.

It is less clear whether the estimates can be improved sufficiently to determine whether the global surface and atmospheric CO<sub>2</sub> repositories vary from year to year. Such variation would be indicative of present-day climate change on Mars. A decreasing surface reservoir of CO<sub>2</sub> has been suggested on the basis of a limited number of high-resolution images of dry ice pits and mesas (11). But the changes were observed only over one Mars year. To determine whether the current trend represents climate change, we ideally need observations over a decade or more.

The style of volatile condensation is another puzzle. There is evidence that CO<sub>2</sub> condenses out of the martian atmosphere both as dry ice snow and as surface frost. However, the relative importance of the two processes remains unknown. Surface condensation in some southern high-latitude regions—termed “cryptic terrain”—appears to result in large slabs of almost transparent dry ice (12). To explain cryptic regions, Kieffer offered a model (13) in which radiative warming of dust grains entrained in slab ice leads to sinking of the dust, which forms a dark substrate at the base of the dry ice layer. He hypothesized that warming and sinking of grains results in venting and jetting of gaseous CO<sub>2</sub> that produces the “dalmatian” spots, spots with halos (“fried eggs”), and ragged channels cut by CO<sub>2</sub> gas (“spiders”).

The complexity may increase further as water is added to the picture. John Longhi (Lamont-Doherty Earth Observatory) noted that the phase equilibria of CO<sub>2</sub>-water

mixtures can explain much of what is unusual on Mars. His calculations (14) showed that during periods of low planetary axial tilt, preferential melting of CO<sub>2</sub> ice and clathrate layers could lead to the sequestration of pockets of liquid CO<sub>2</sub> in the martian crust. These pockets could erupt explosively when coming in contact with ground water or ice.

Abundant water ice in the shallow subsurface of Mars, concentrated at high latitudes of both hemispheres, continues to fascinate both planetary and terrestrial scientists. In this case, terrestrial experience with subsurface water ice provides some intuition. The latest results from the neutron (4, 5) and gamma-ray (6) spectrometers on the Mars Odyssey spacecraft confirm last year’s discovery of surprisingly high water ice contents (>50 weight %) in the upper meter of the ground at high martian latitudes.

Given the low present-day abundance, such a high ice content is inconsistent with water ice simply freezing out of the atmosphere. On the basis of studies of ice-rich soils on Earth, William Boynton (University of Arizona) argued that the high ice concentrations result from many condensation and dust deposition cycles and must have occurred when the atmospheric water content of Mars was much greater than it is today (6). If ice-rich zones in the shallow martian substrate formed in response to more than a single deposition event, the task of relating the sequential layering of bright ice-rich layers and dark dust-rich layers to specific seasonal or climatic cycles is likely to be more difficult than previously believed.

Resolving the puzzling nature of mar-

tian polar processes will require progress on numerous fronts. Surface temperature and pressure observations are key to characterizing seasonal variability. Obtaining these data will require a network of meteorological stations on the martian surface. But progress can also be made with less ambitious means. For example, conference participants considered laboratory studies of the rheological, thermophysical, and electromagnetic properties of water-CO<sub>2</sub> mixtures to be of high priority.

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## PLANT SCIENCES

# Deciding When to Flower

Ruth Bastow and Caroline Dean

One of the most important developmental decisions in a plant’s life is when to switch from vegetative to floral (reproductive) growth. If flowering is initiated at the wrong time of the year, it will affect the number of seeds produced and significantly reduce reproductive success. When to flower is therefore a critical decision, and consequently multiple mechanisms have evolved to align flowering with optimal environmental conditions. But how does a plant recognize the pres-

ence of favorable conditions and integrate this information with its own endogenous developmental program? A new clue to this problem comes from the work of He *et al.* (1) reported on page 1751 of this issue.

To dissect the molecular processes that initiate flowering and trigger the change from vegetative to reproductive growth, biologists have carried out intensive genetic studies of flowering time in the model plant *Arabidopsis* (2). This has led to the discovery of many genes involved in the regulation of flowering time and the development of a number of genetic models. Despite progress in identifying the genetic pathways involved, the mechanisms by which these flowering gene products modulate the

floral transition is largely unknown. He *et al.* (1) now elucidate one mechanism by which plants regulate flowering time. They identify a protein called FLOWERING LOCUS D (FLD), which removes acetyl groups from (deacetylates) histone proteins in chromatin containing the *FLOWERING LOCUS C* (*FLC*) gene. The FLC protein encoded by this gene is a member of the MADS-domain family of transcription regulators and is a strong repressor of flowering (3, 4). By deacetylating histones in *FLC* chromatin, FLD prevents transcription of FLC enabling the plant to flower.

To ensure that flowering occurs at the correct time in *Arabidopsis*, floral initiation is regulated by the integration of signals from developmental pathways and environmental cues. These include pathways that monitor plant hormones, detect light quality and duration, and respond to prolonged exposure to cold (vernalization). A number of these pathways converge on the common target *FLC*.

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The autonomous promotion pathway regulates flowering independently of photoperiod (hence its name) by repression of *FLC* expression. FLD is one of six identified members of the autonomous pathway. Like other mutants in this pathway, *fld* mutants exhibit delayed flowering due to an increase in production of the flowering repressor *FLC*.

In their new work, He and colleagues show that FLD is homologous to the human protein KIAA060, a component of the hu-

man Histone Deacetylase 1,2 (HDAC 1/2) complex. HDAC complexes remodel chromatin by removing acetyl groups from lysine residues in the tails of histones (5). Hyperacetylated histones are associated with transcriptionally active genes, and hypoacetylated histones with transcriptionally silent chromosomal regions. To examine whether FLD may be a component of a plant HDAC complex, He and co-workers studied the acetylation state of histone H4 at the *FLC* locus. They immunoprecipitated specific chromatin fractions with an antibody against acetylated H4 histone tails and inspected the different fractions using polymerase chain reaction—a technique called chromatin immunoprecipitation (ChIP). They found that

in *fld* mutants of *Arabidopsis*, histone H4 tails in a specific region of the *FLC* locus are hyperacetylated compared with those in wild-type plants. So, when the deacetylating activity of *FLD* is disrupted, *FLC* remains acetylated and is actively transcribed, resulting in a delay in flowering.

HDACs are often recruited to their targets through interactions with cis-regulatory elements. To define these cis-elements, He and co-workers generated a series of inter-

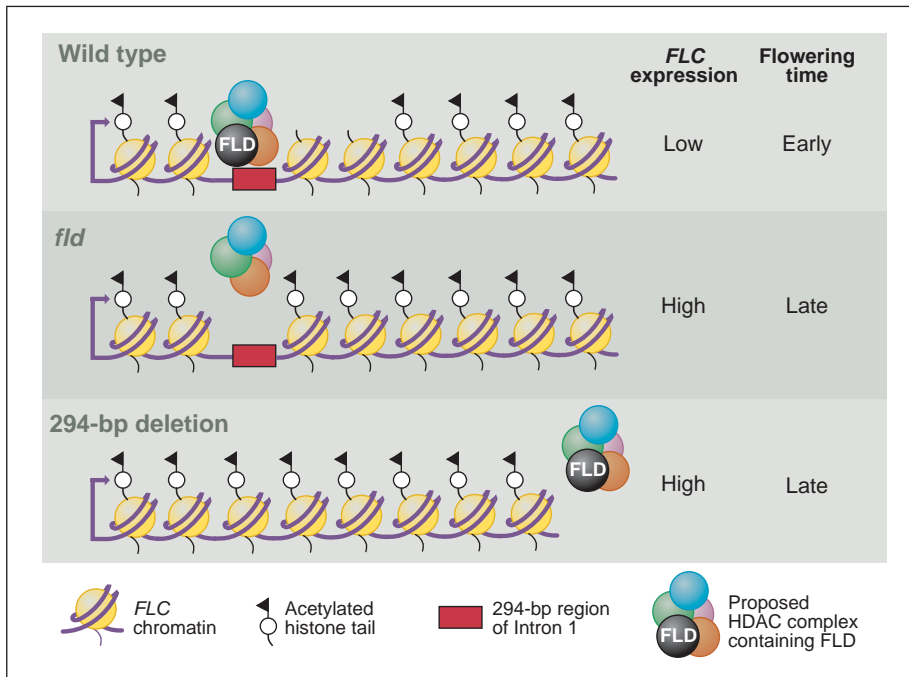
actions at the *FLC* locus. The autonomous pathway, therefore, must exploit multiple mechanisms to regulate *FLC*. Other components of the autonomous pathway include *LD*, which encodes a homeodomain protein (6); *FPA* and *FCA*, which encode RNA-binding proteins (7, 8); and *FY*, which encodes a polyadenylation factor (9). However, the exact mechanism by which these components regulate *FLC* is still not known. Further studies examining how FLD regulation of *FLC* is integrated with information from other pathways modulating *FLC* will provide a useful model for understanding how regulatory networks converge on a single target.

Although the homology of FLD to a component of the mammalian HDAC1/2 complex would imply that FLD is part of a similar complex in plants, this still needs to be demonstrated. Four genes with homology to HDAC1/2 have been found in the *Arabidopsis* genome. However, the effects of mutations in these genes do not resemble those in *fld* mutants. This may reflect redundancy among the HDACs such that no one mutation alters flowering time. Consistent with this, treatment with an antisense transgene that is likely to suppress several of the HDACs does result in late flowering (10). The discovery of multiple *FLD* homologs in *Arabidopsis* raises the possibility that different FLD-like proteins are part of HDAC complexes with different target-site specificities.

The He *et al.* study encourages further analysis of the presumptive FLD complex, which should provide a greater understanding of the evolutionary conservation of its constituent proteins and their involvement in transcriptional repression in both plants and mammals. Such an analysis may also reveal the ways in which plant development is more plastic and adaptable than animal development. Many plant cells are totipotent, so plants need versatile mechanisms to reprogram chromatin states. Many tools are now in hand to dissect these mechanisms and to address how they differ from those controlling reprogramming of animal genomes.

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**Chromatin regulation and flowering.** Regulation of the floral repressor *FLC* by FLD. Shown are the acetylation states of *FLC* chromatin in wild-type plants (top), *fld* mutants (middle), and plants lacking a specific 294-bp region of *FLC* intron 1 (bottom). **(Top)** In wild-type plants, FLD acts as part of an HDAC complex, which interacts directly or indirectly with intron 1 of *FLC* to deacetylate specific regions of its chromatin. Consequently, *FLC* expression is reduced and the plant is able to flower. **(Middle)** In plants lacking functional FLD, FLD-dependent deacetylation of *FLC* is lost. Presumably, the HDAC complex containing mutant FLD can no longer be targeted to *FLC*. Therefore, the *FLC* locus remains acetylated, is actively transcribed, and flowering is delayed. **(Bottom)** Removal of a 294-bp region of *FLC* intron 1 also prevents FLD-dependent deacetylation of this locus possibly because the HDAC complex can no longer bind to *FLC*. Thus, *FLC* remains acetylated, and the gene is expressed, with a consequent delay in flowering.

man Histone Deacetylase 1,2 (HDAC 1/2) complex. HDAC complexes remodel chromatin by removing acetyl groups from lysine residues in the tails of histones (5). Hyperacetylated histones are associated with transcriptionally active genes, and hypoacetylated histones with transcriptionally silent chromosomal regions. To examine whether FLD may be a component of a plant HDAC complex, He and co-workers studied the acetylation state of histone H4 at the *FLC* locus. They immunoprecipitated specific chromatin fractions with an antibody against acetylated H4 histone tails and inspected the different fractions using polymerase chain reaction—a technique called chromatin immunoprecipitation (ChIP). They found that

nal deletions of the *FLC* gene and introduced them into plants lacking functional *FLC*. Removal of a 294-base pair (bp) region within intron 1 of *FLC* promoted hyperacetylation of *FLC* chromatin, *FLC* expression, and late flowering (see the figure). Thus, deletion of this specific region of intron 1 has effects on *FLC* expression similar to those observed in *fld* mutant plants.

Taken together these results show that FLD regulates *FLC* by deacetylating histones in *FLC* chromatin, providing evidence for chromatin regulation of *FLC* expression. The other components of the autonomous pathway also down-regulate *FLC* expression. But He *et al.* demonstrate that, with the exception of *FVE*, they do not cause similar