

PLANT SCIENCE

Standing on the Shoulders of GIGANTEA

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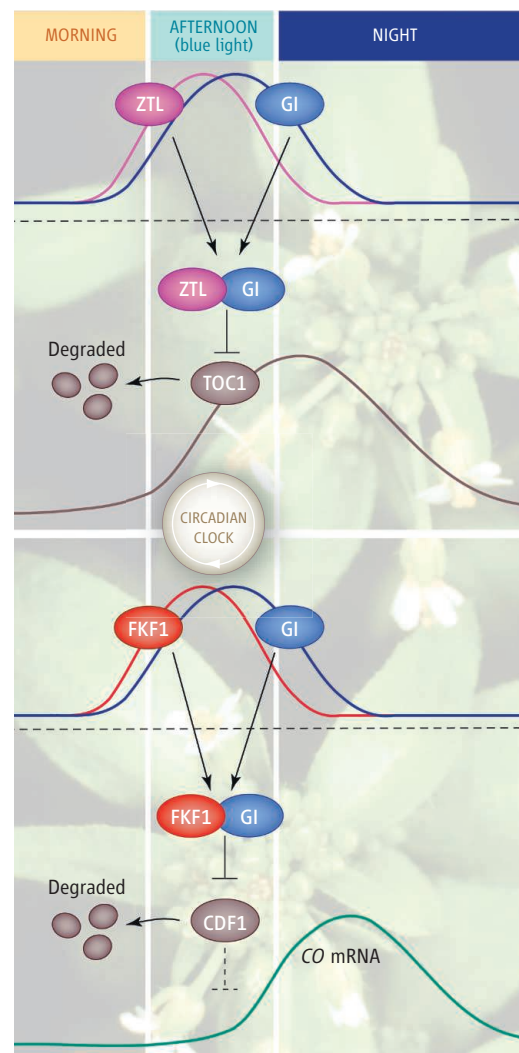
Recognizing seasonal change allows many plant species to select the most favorable time of the year to flower, thereby increasing the chances of their reproductive success. To recognize these transitions, a plant measures variations in day length and compares them with its circadian clock, an internal molecular oscillator that controls daily biological rhythms, such as leaf movements and the opening of stomata, pores in the plant's leaves (1). However, the molecular mechanisms underlying this coordination are still largely missing. Now, Sawa *et al.* on page 261 of this issue (2) and a recent study by Kim *et al.* (3) bring us a big step closer toward characterizing such mechanisms by identifying two light-sensing molecular switches that directly control flowering and clock oscillation.

Molecular genetic studies performed in the plant *Arabidopsis thaliana* have shown that photoperiodic flowering and regulation of the circadian clock share common elements, including light receptors and proteins comprising the circadian timekeeper (1). The light receptors include the phytochromes and cryptochromes, which control both clock resetting and flowering in response to different wavelengths of light (4). Members of the ZTL-FKF1-LKP2 protein family [consisting of ZEITLUPE (ZTL), FLAVIN-BINDING, KELCH REPEAT, F-BOX 1 (FKF1), and LOV KELCH PROTEIN 2 (LKP2)] are also proposed to act as receptors that mediate light input to the clock (5–7).

The ZTL-FKF1-LKP2 proteins contain a light, oxygen, or voltage (LOV) domain, which likely functions as a blue light-sensing motif, and an F-box domain (8). F-box-containing proteins are usually part of complexes that attach ubiquitin molecules to protein targets to promote their destruction in a structure called the proteasome. The presence of LOV and F-box domains suggests roles for this protein family in transducing light into intracellular signals through the degradation of key proteins. Indeed, FKF1 and ZTL regulate

flowering time and circadian rhythms by controlling the protein stability of CYCLING OF DOF FACTOR 1 (CDF1), a transcriptional repressor of flowering, and the oscillator component TIMING OF CAB 1 (TOC1), respec-

Plants translate the sensation of light into the regulation of protein interactions that directly control their internal molecular clock mechanism and the time of flowering.



When to flower? (Upper panel) The plant circadian clock controls rhythmic expression of the GI protein, whose interaction with ZTL is stabilized by blue light. ZTL-GI interaction controls accumulation of the clock component TOC1, thus allowing robust circadian oscillations in gene expression. **(Lower panel)** Blue light also induces formation of an FKF1-GI protein complex, which in turn targets CDF1, a transcriptional repressor of flowering, for degradation. CDF1 proteolysis releases transcriptional repression of the *CO* gene, which allows CO protein expression and long day-dependent accumulation to promote flowering.

tively (9, 10). Accordingly, mutations in the *FKF1* and *ZTL* genes delay flowering under favorable conditions (long days) and alter expression of genes controlled by the circadian clock. Similar effects are caused by lack of *GIGANTEA* (GI), a protein that controls clock oscillations and photoperiodic flowering, but whose precise biochemical activity in these processes has remained unknown (11).

Similarities in the function and rhythmic expression of FKF1 and GI prompted Sawa *et al.* to analyze possible regulatory relationships between these two proteins by looking for their physical interactions in plants. To do so, they used *Arabidopsis* transgenic plants that expressed epitope-tagged versions of GI and FKF1. Such tagging allowed them to use epitope-specific antibodies to detect the tagged proteins in plant extracts. The authors found that both proteins precipitated together, indicating that FKF1 and GI associate in a complex in vivo. The interesting thing is that their interaction occurred differentially throughout the day, peaking in the afternoon during both long and short days, and diminishing at night. Moreover, they found that the FKF1-GI interaction was induced by blue but not red light, and that the LOV domain in FKF1 was responsible for blue light absorption, demonstrating that FKF1 functions as a blue light receptor.

In accordance with light requirement, FKF1-GI association was disrupted in the dark and was very rapidly induced upon light exposure. The latter response coincided with quick induction of the expression of *CONSTANS* (*CO*), a gene encoding a positive regulator of flowering, whose transcription is impaired by the flowering repressor CDF1. An FKF1-GI-CDF1 complex was detected on the promoter region of the *CO* gene, which suggests that the association of FKF1 and GI causes CDF1 to release its repression of *CO* expression, thus promoting flowering. These results unveil the molecular basis

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of how photoperiodic flowering is controlled by the coincidence of light with circadian timing [the so-called external coincidence model (1)].

By analyzing the phenotype of plants with mutations in *FKF1* and *GI*, Sawa *et al.* determined that GI function in photoperiodic flowering does not completely depend on FKF1. Thus, GI may regulate the activity of other ZTL-FKF1-LKP2 family members or that of additional proteins controlling circadian clock functions. The demonstration of such a possibility comes from a complementary study by Kim *et al.* (3) describing the relationship between GI and ZTL. Kim *et al.* show that GI interacts with ZTL in plants and that ZTL-GI complex formation is, as in the case of FKF1, triggered by blue light. Interaction between GI

and ZTL cooperatively stabilized both proteins, thereby increasing their accumulation. This increase consequently amplified and sharpened the rhythmic expression profile of the clock protein TOC1, thus providing the clock oscillator with the robustness necessary to maintain proper circadian rhythms.

Both Sawa *et al.* and Kim *et al.* provide mechanistic views on how day-night cycles shape circadian clock oscillations and how light is integrated into the clock to precisely regulate expression of a gene (*CO*) that controls flowering. The studies raise many questions: What factors control ZTL, FKF1, and GI stability? What role(s) do other light receptors (phytochromes and cryptochromes) play in controlling light signaling to the clock? Are there more targets for the GI-containing com-

plexes? These insights will help us to better understand why plants see changes in seasons by standing on the shoulders of GIGANTEA.

References

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10.1126/science.1150213

MATERIALS SCIENCE

Crackling Wires

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Take a paper clip, and pull one of the ends sideways. If you pull gently and release, it will elastically rebound to its original shape like a spring. If you pull harder, it deforms permanently into a new shape, a process called yielding. On page 251 of this issue, Csikor *et al.* (1) provide convincing theoretical evidence that, rather than a smooth process, yielding is like a phase transition that consists of a series of small avalanches. These avalanches not only provide the microscopic underpinnings we need to build theories of how ordinary-sized objects bend, but Csikor *et al.* further argue that the avalanches become crucial problems for controlling bending on micrometer and nanometer scales (see the figure).

Phase transitions are either abrupt or continuous. For example, the melting transition (solid to liquid) and the boiling transition (liquid to gas) are usually abrupt; water is water until at 0°C it turns to ice. Brittle materials respond to external stress in a similarly abrupt fashion; a piece of glass will bend elastically until abruptly it breaks in two. In contrast, magnets gradually reduce their magnetization as they are heated, with the magnetization smoothly going to zero at the critical temperature. Superconductors, superfluids, and some liquid crystals also change phases in a continu-

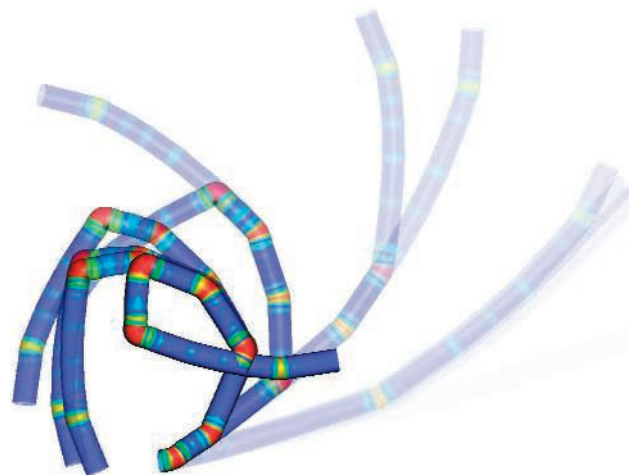
ous fashion. Near continuous phase transitions there are dramatic fluctuations; the material doesn't know which phase to choose, so it wanders in space and time among its options.

In the past few decades, physicists found that the characteristic features of continuous thermodynamic (temperature-driven) phase transitions are also found at so-called depinning (force-driven) transitions—continuous transitions between a stuck (“pinned”) and moving phase as an external force is increased. Depinning has been studied in many systems (2, 3): charge-density waves in electric fields, fluids invading porous media (milk being poured into breakfast cereal), tearing of paper, superconductors with large currents, and domain walls in magnets. Here the fluctuations near the transition take the form of avalanche-like motions, resulting in crackling noise (4). A good example is provided by the response of the Earth's crust to the motion of the tectonic plates—earthquakes are avalanches driven by the forces across fault lines. If you speed up the seismic recordings of earthquakes from 1 year to occupy a single second, they sound like crackling noise (5).

Wires bend through a series of tiny avalanches as defects move through the material.

The characteristic power-law distribution of earthquakes, with many small ones and few large ones, has analogs in all of these other depinning systems.

What about paper clips? The yielding of crystals can be viewed as the depinning of tangles of dislocation lines (flaws in the crystalline lattice structure). But rather than concentrating on deformation of materials, physicists have focused on relatively obscure cases



Miniature avalanches. Csikor *et al.* predict that bending a 0.1- μm -wide aluminum wire will be an irregular, jerky process, dominated by a few large dislocation avalanches that span the width of the wire. The different images show the progression of bending. The color scale shows the local amount of deformation (blue is low, red is high). Note that the red regions are introduced one by one (individual avalanches).