Meeting report

A weed for all reasons

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A report on the 16th International *Arabidopsis* Conference, Madison, USA, 15-19 June 2005.

This year's meeting on the model plant *Arabidopsis* highlighted the progress that has been made in many areas of its biology by the use of a variety of genetic and genomic tools. One recurring theme was how multiple layers of transcriptional and posttranscriptional regulation are integrated to produce a biological response.

Triggers for flowering

Particularly notable was the progress in understanding how flowering time is regulated by extrinsic and intrinsic signals (Figure 1). In some *Arabidopsis* winter annual cultivars, a cold period is required to induce flowering (a phenomenon known as vernalization), as reviewed by Rick Amasino (University of Wisconsin, Madison, USA). Extended cold leads to a stable epigenetic change that results in histone methylation at the *FLOWERING LOCUS C* (*FLC*) gene, which encodes a repressor of flowering. The histone methylation silences *FLC* expression, thus rendering the FLC repressor mechanism inactive and making the plants competent to flower. Modulation of *FLC* expression is thus key to the process of vernalization. Amasino described a novel allele of *FLC* that is permanently inactive as a result of the insertion of a heterochromatic island in an intron, and showed that maintenance of the heterochromatic state is mediated by short interfering RNAs (siRNAs). Another mode of *FLC* regulation is through the gene *VERNALIZATION INSENSITIVE 3* (*VIN3*), which is required for the initiation of *FLC* histone methylation. Amasino presented a model suggesting that *VIN3* is activated when a threshold is passed as a result of cold treatment. The mechanisms involved in distinguishing between long and brief periods of cold are, however, still far from being understood - for example, what triggers this response after several weeks of cold, but not a few days?

One of the targets of the FLC transcription factor is the *FLOWERING LOCUS T* (*FT*) gene, which promotes flowering. George Coupland (Max Planck Institute for Plant Breeding Research, Cologne, Germany) described another route by which *FT* expression is regulated, by integrating inputs from day length and the circadian clock. These modulate the expression of the gene *CONSTANS* (*CO*), which in turn activates *FT* expression. *CO* is regulated at the transcriptional level by the circadian clock, and at the post-transcriptional level by daylength. Coupland described how CO protein is degraded in the dark in a proteasome-dependent process. This degradation is likely to be mediated by the action of the CONSTITUTIVE PHOTOMORPHOGENESIS 1 (COP1) ubiquitin E3 ligase, as CO and COP1 co-localize in dark conditions.

Coupland also explored the site of action of these proteins. Flowering occurs in response to changes in the shoot meristem, yet grafting experiments have shown that the flowering signal is perceived in leaves. Driving either *CO* or *FT* expression in the phloem, using the *SUC2* promoter, results in early flowering. He showed, using FT tagged with green fluorescent protein (GFP), that the FT protein remains in the phloem, indicating that events downstream of FT must be responsible for changes occurring at the meristem. Michitaka Notaguchi (Kyoto University, Japan) has taken a different approach and he reported that the FT signal is graft-transmissible. Together, these results suggest that FT is required in the leaf to regulate the production of a transmissible signal that can then move to the meristem to effect flowering.

A large-scale screen to find transcription factors involved in regulating flowering time was also described by Coupland. The transcription factors were overexpressed using several different promoters, and one gene identified, *FIDGET*,

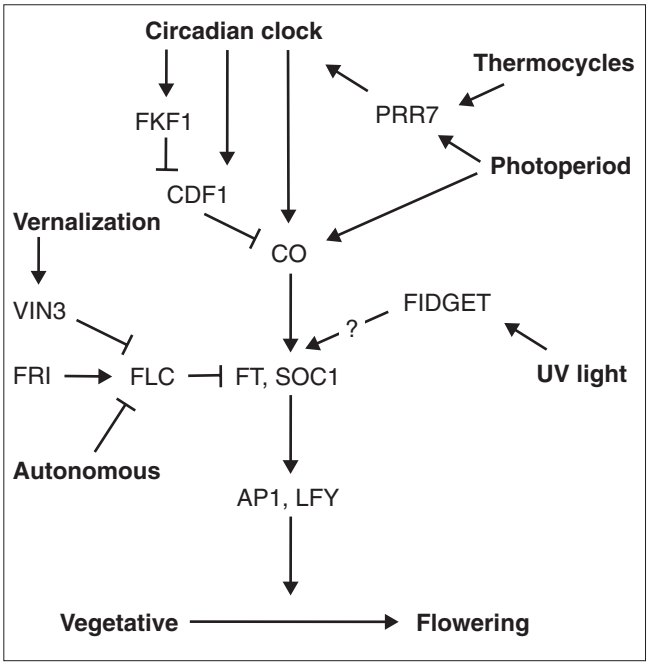

Figure 1
A diagrammatic representation of some proteins important for the integration of internal and external signals that control flowering time by influencing the transition from vegetative to flowering growth. The autonomous pathway is independent of environmental cues and depends on an endogenous program of development to regulate flowering. Proteins involved in the responses to photoperiod and circadian signals include PSEUDO-RESPONSE REGULATOR 7 (PRR7), FLAVIN-BINDING, KELCH REPEAT, F-BOX 1 (FKF1), CYCLING DOF FACTOR 1 (CDF1) and CONSTANS (CO). The vernalization pathway is mediated in part by VERNALIZATION INSENSITIVE 3 (VIN3), FRIGIDA (FRI), and FLOWERING LOCUS C (FLC). Ultraviolet (UV) light may act through FIDGET. These inputs appear to be integrated by FLOWERING LOCUS T (FT) and SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1 (SOC1) that in turn act through APETALA1 (AP1) and LEAFY (LFY) to regulate flowering. See text for details.

caused early flowering even in loss-of-function *co* mutants, suggesting that FIDGET is either functioning downstream of, or in parallel to, CO. *FIDGET* expression is induced by ultraviolet light, suggesting that the FIDGET protein may define a stress-induced flowering pathway.

Continuing the theme, Steve Kay (Scripps Research Institute, La Jolla, USA) described recent work dissecting the mechanisms by which CO is regulated. The gene *FKF1* encodes an F-box factor that is part of the SCF complex (an E3 ubiquitin ligase) involved in modulating *CO* expression. Kay's group has identified CYCLING DOF FACTOR 1 (CDF1), a transcription factor that is a target of FKF1-mediated protein degradation. CDF1 directly binds to the promoter of *CO* and negatively regulates its expression. Both *CDF1* and *FKF1* are circadian-regulated genes but *CDF1* transcripts peak in the morning and decline through the day whereas *FKF1* peaks in the late afternoon, resulting in CDF1 degradation. The combined effects of transcriptional and posttranscriptional regulation of these genes results in a fine tuning of CO protein accumulation under different daylength regimes.

Naturally occurring genetic variation is a rich source of novel alleles of key regulatory genes. Rob McClung (Dartmouth College, Hanover, USA) demonstrated the utility of exploiting natural variation to identify circadian clock genes. This led to the identification of a locus corresponding to *PRR7*, a previously identified gene required to entrain the clock in response to thermocycles (the daily variation in temperature) as well as photoperiod (daily variation in light). *PRR7* shows a great deal of variation across *Arabidopsis* accessions and appears to be undergoing strong diversifying selection, and so may be responsible for synchronizing clock responses and environmental conditions.

Regulatory RNAs

MicroRNAs as regulators of gene expression are being found in plants as well as animals and appear to be involved in a variety of processes. These include the establishment of adaxial (towards the shoot tip)-abaxial (away from the shoot tip) polarity. Kiyotaka Okada (Kyoto University) described a microRNA (miRNA) sensor system developed to identify the localization of specific miRNAs. This involves engineering a *35S::GFP* construct (35S being a commonly used constitutive promoter) containing a miRNA target sequence from the *PHABULOSA (PHB*) gene, a gene involved in establishing the adaxial-abaxial axis. Despite being constitutively transcribed, the GFP signal was restricted to the adaxial region, indicating that *PHB*-specific microRNAs are functioning and reaching the target sequence in the abaxial domain. Okada also showed that the *PHB* promoter is sufficient to direct adaxial-specific gene expression, albeit in a broader domain, suggesting that the *PHB*-targeted miRNA works to fine tune expression boundaries.

RNA is also brought into the picture to explain recent results suggesting that *hothead* mutants of *Arabidopsis* can revert to ancestral sequences not present in the genomes of the parents, as reviewed by Susan Lolle (Purdue University, West Lafayette, USA). The inference is that this non-Mendelian inheritance relies on an RNA cache of such sequences that appears to be maintained for at least five generations. Determining how long such a cache can be maintained, as well as determining the physical extent of such reversion events, will be key in defining the molecular basis for this provocative hypothesis.

Signal successes

Protein localization and degradation were emphasized once again in explaining the role of the plant hormone auxin. Tomasz Paciorek (University of Tübingen, Germany) pre-

sented results showing that auxin affects the localization of the PIN auxin-efflux proteins, which mediate the transport of auxin out of a cell. Auxin decreases the rate of endocytosis, resulting in an increased concentration of PIN protein in the plasma membrane. This observation is exciting as it provides an explanation of how auxin has a positive effect on its own transport. It is also the first example of a plant hormone regulating protein localization by modifying endomembrane trafficking. Gerd Jürgens (University of Tübingen) elaborated on the importance of the dynamic localization of PIN proteins with regard to embryogenesis. He discussed the significance of PIN7 protein relocalization in causing active degradation of BODENLOS (a short-lived protein that inhibits the action of auxin), thus allowing the function of its partner MONOPTEROUS (ARF5), a transcription factor that acts on auxin-responsive genes.

The dissection of signaling pathways involved in self-incompatibility (the inability of a plant's pollen to fertilize its own ovules) was discussed by June Nasrallah (Cornell University, Ithaca, USA), who summarized her group's elegant work characterizing the molecular basis of this phenomenon. In *Brassica oleracea*, a self-incompatible close relative of *Arabidopsis*, self-incompatibility depends on allele-specific interactions between a pollen-borne ligand and a receptor kinase expressed on the female flower part, the stigma. The receptor and ligand must coevolve to maintain this interaction and, given the extensive variability in these components within a species, there must be a strong selective advantage to developing and maintaining new specificities. Nasrallah described recent work on converting the normally self-compatible *Arabidopsis thaliana* into a self-incompatible system by introducing the incompatibility genes from *Arabidopsis lyrata*. This has allowed her group to carry out genetic screens to identify incompatibility signal transduction components. At least one interesting gene involved in the appropriate timing of the self-incompatibility response has been identified.

The utility of a chemical genomics approach for probing signaling processes was emphasized by Natasha Raikhel (University of California, Riverside, USA). A vast number of potential small molecules could affect signaling, and by prescreening such molecules in yeast, her group has identified several bioactive agents that affect protein localization not only in yeast but also in *Arabidopsis*. In turn, these molecules have facilitated screens for hypersensitive mutations that affect endomembrane trafficking. Raikhel pointed out that such research is easily translatable between systems, as one can identify relevant bioactive compounds and then directly apply such compounds to crop species of interest.

As Chris Somerville (Stanford University, USA) stressed in his keynote address, however, *Arabidopsis* is not just a model for crop improvement. Plants harness solar energy and, as such, plant biomass can provide a cost-effective means of dealing with global energy concerns. Thus, the many tools now available for probing *Arabidopsis* biology should provide us with strategies not only to improve agriculture but also to secure our energy needs in the future.