EMBO *reports*

meeting report

Plant research accelerates along the (bio)informatics superhighway

Symposium on Plant Sensing, Response and Adaptation to the Environment

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The Keystone Symposium on Plant Sensing, Response and Adaptation to the Environment took place between 11 and 16 January 2009, at Big Sky, Montana, USA, and was organized by S.A. Kay & J. Chory.

Keywords: abiotic; biotic; circadian; genomics
EMBO *reports* (2009) **10**, 568–572. doi:10.1038/embor.2009.116

See Glossary for abbreviations used in this article.

Introduction

In spite of the fanfare surrounding the two-hundredth anniversary of the birth of Charles Darwin, and the one-hundred and fiftieth anniversary of his most celebrated book '*On the Origin of Species*' (Darwin, 1859), many people would still be surprised to learn that Darwin wrote a nearly 600 page book entitled '*The Power of Movement in Plants*' (Darwin, 1880). As most plants have their location fixed as soon as their roots enter the soil, non-specialists might wonder how much movement plants can make. However, movement is not limited to locomotion, and many of the movements studied by Darwin probably evolved in response to the unique challenges imposed by the rooted habit. Unable to change location, plants have developed exquisite abilities to sense, respond to and adapt to their local environment. One example that captured Darwin's attention is the navigation of the radicle (root) tip through the complex soil environment to optimize water and nutrient acquisition. He stated, "It is hardly an exaggeration to say that the tip of the radicle thus endowed, and having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals[…]."

These root-growth movements were but one of many environmental responses discussed by plant biologists gathered at the recent Keystone Symposium on Plant Sensing, Response and Adaptation to the Environment. Root growth is controlled by gravity, water and nutrient acquisition; whereas growth of the aerial shoot is regulated primarily by the light environment. Various photoreceptors allow plants to judge light intensity, direction and competing vegetation, and responses to these cues modify plant growth to maximize photosynthetic input. In addition, plants perceive and respond to many abiotic and biotic stresses, including drought, cold, heat, salt, animal herbivory and microbial pathogens. Fundamental to plant sensing and responding to the environment is the circadian oscillator (Hotta *et al*, 2007)—informally known as the clock. Similar to most organisms, plants have an internal oscillator with a periodicity of approximately 24 h. This oscillator allows plants to prepare for daily changes in the environment; for example, by upregulating photosynthetic genes before dawn. The clock also regulates (gates) the sensitivity to environmental inputs; for example, cold-responsive genes are most inducible at dusk. In addition, clocks allow photoperiod measurement, and therefore regulate seasonal responses such as flowering and bud set.

The symposium gathered scientists with expertize in various aspects of plant environmental responses at levels ranging from biochemical mechanisms to ecology and genomics. The extent of cross-disciplinary studies described at the meeting was particularly

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Submitted 13 March 2009; accepted 21 April 2009; published online 22 May 2009

rewarding. A true understanding of biochemical mechanisms must be informed by evolutionary and ecological knowledge, and vice versa. The meeting illustrated that we have entered an age in which information flow—fuelled by genomics and informatics—has markedly increased among researchers, disciplines and organisms, thereby benefiting all fields (Fig 1). We have structured this report around the different aspects of information flow: foundational studies, acquisition, transfer and modelling.

Foundation of information: mechanisms

The information highway depends on detailed mechanistic studies that define protein function and signalling mechanisms. Such studies lay an essential foundation for more comparative and high-throughput methods.

Several talks focused on the mechanisms of light perception. An important part of any environmental response pathway is the attenuation of signalling after stimulation; this topic was discussed by W. Briggs (Palo Alto, CA, USA), who described the association of PP2A with the PHOT2 photoreceptor. Activated PHOT2 usually reverts to an inactive form within minutes of transfer to darkness, which is a process associated with PHOT2 dephosphorylation. Briggs showed that dark reversion requires PP2A: mutants that reduced PP2A activity had reduced PHOT2 reversion, accompanied by enhanced phototropism and stomatal opening. He reported a different attenuation mechanism for PHOT1: PHOT1–GFP is localized to the plasma membrane in plants grown in darkness but rapidly translocates to cytoplasmic speckles after exposure to blue light. Briggs found that red-light pretreatment—sensed by the photoreceptor phytochrome (PHY) A—prevented PHOT1 translocation, allowing it to stay in an active signalling location for longer (Han *et al*, 2008), thereby explaining the long-standing observation that red-light pretreatment enhances phototropism. C. Fankhauser (Lausanne, Switzerland) investigated the attenuation of phytochrome signalling. In the dark, phytochromes are cytoplasmic and light induces their translocation to the nucleus where they bind to and promote the degradation of bHLH transcription factors known as PIFs. Previous work from the Fankhauser group has shown that PIF4 and PIF5 function downstream of PHYB to activate transcription transiently in response to a low ratio of red-to-far-red light, which occurs when plants are shaded by a chlorophyll-containing leaf (Lorrain *et al*, 2007). At the symposium, Fankhauser reported that the activation is transient because an atypical bHLH protein, HFR1, is induced by leaf shade and subsequently heterodimerizes with PIF4 or PIF5 to prevent the binding of PIF to target gene promoters. Relatively little is known about the earliest events that occur in phytochrome signalling, before translocation to the nucleus where it localizes to nuclear bodies and interacts with PIFs. J. Chory (La Jolla, CA, USA) described a screen for mutants that are defective in the localization of PHYB–GFP to nuclear bodies. One such mutant, *hmr*, is defective in all aspects of phytochrome signalling; this phenotype is seen only in seedlings with mutations that disrupt chromophore photosynthesis, indicating that *HMR* acts close to phytochrome activation.

The mechanisms of circadian clock function were also a popular subject. T. Kondo (Nagoya, Japan) presented the latest on the pioneering *in vitro* oscillator that his laboratory has reconstituted from three cyanobacterial Kai proteins (Nakajima *et al*, 2005). One characteristic of circadian oscillators is that they are entrainable by external stimuli; remarkably, Kondo showed that the simplified *in vitro* Kai system is temperature entrainable (Yoshida *et al*, 2009).

Glossary

bHLH	basic helix–loop–helix motif
CCA1	CIRCADIAN CLOCK-ASSOCIATED 1
CHE	CCA1 HIKING EXPEDITION
CO	CONSTANS
FKF1	FLAVIN-BINDING KELCH REPEAT, F-BOX 1
FLC	FLOWERING LOCUS C
FT	FLOWERING LOCUS T
GFP	green fluorescent protein
GI	GIGANTEA
HFR1	LONG HYPOCOTYL IN FAR RED 1
HMR	HEMERA
LHY	LATE ELONGATED HYPOCOTYL
LOV	light oxygen voltage
PEP1	PERPETUAL FLOWERING 1
PHOT	PHOTOTROPIN
PIF	PHYTOCHROME-INTERACTING FACTORS
PP2A	PROTEIN PHOSPHATASE 2A
RVE1	REVEILLE 1
TCP	TEOSINTE BRANCHED 1, CYCLOIDEA AND PCNA FACTORS
TOC1	TIMING OF CAB EXPRESSION 1
ZTL	ZEITLUPE

He also demonstrated that the intrinsic periodicity of the oscillator is determined by the rate of KaiC ATPase activity (Kitayama *et al*, 2008). Moving on to the *Arabidopsis* clock (Fig 2), T. Imaizumi (Seattle, WA, USA) presented work on the photoreceptor FKF1, which is important for the photoperiodic control of flowering (Imaizumi *et al*, 2005). Although overexpression or loss-of-function mutations of FKF1 have little effect on clock function, double mutants of *fkf1* and its homologue *ztl* were found to have a clock period that was significantly longer than either single mutant, establishing a function for FKF1 in the regulation of the oscillator itself. E. Tobin (Los Angeles, CA, USA) discussed the development of alcohol-inducible constructs to test whether the pulsed expression of clock components can shift the circadian phase. Pulses of CCA1 and LHY caused phase shifts, whereas TOC1 did not, possibly owing to its post-transcriptional regulation (Knowles *et al*, 2008). The regulation of processes that are downstream of the clock was discussed by S. Harmer (Davis, CA, USA). The gene *RVE1* encodes a transcription factor with homology to the core clock component *CCA1*; however, unlike *CCA1, RVE1* functions downstream of the core oscillator. Both CCA1 and RVE1 promote cell elongation, although CCA1 does so through the bHLH transcription factors PIF4 and PIF5, whereas RVE1 promotes growth through the regulation of auxin availability.

Cargo for the highway: information gathering

Recent advances in technology are transforming the study of plant genetics. Researchers now have the ability to obtain data using methods that are orders of magnitude faster, more accurate and less expensive than those available even 5 years ago. Whole-genome sequencing and analysis techniques are allowing researchers to untangle obscure regulatory cascades that underlie the interactions between plants and their environment. S. Kay (La Jolla, CA, USA) and collaborators are developing a collection of vectors that contain most of the known *Arabidopsis* transcription factors. By performing yeast one-hybrid screens using this tool, Kay identified CHE, which is a TCP transcription factor that binds specifically to the promoter of

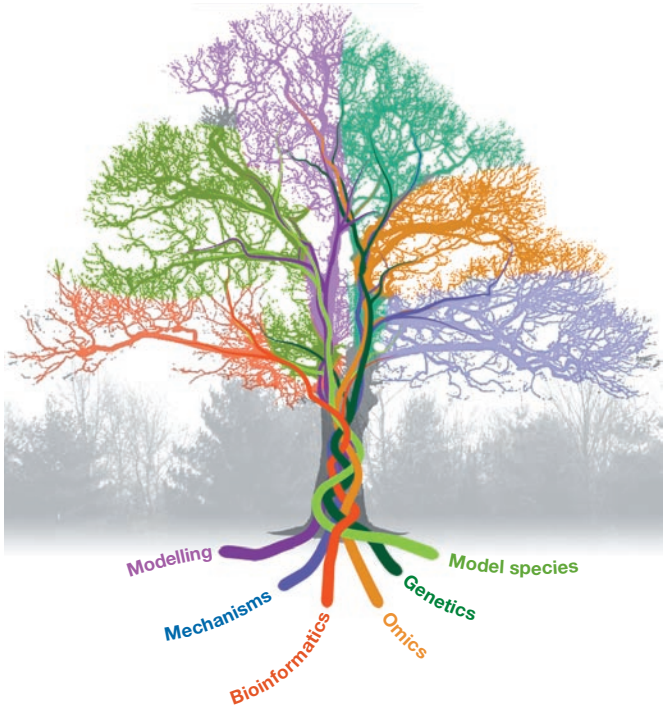

Fig 1 | The flow of plant research information. Information at many levels is being gathered, interleaved and dispersed, transforming our understanding of plant perception and response to the environment.

CCA1 and interacts with TOC1 to regulate circadian rhythms (Fig 2; Pruneda-Paz *et al*, 2009).

Two important resources being developed are the genome sequences of 1,001 *A. thaliana* strains and those of the close relative *A. lyrata*, as presented by D. Weigel (Tübingen, Germany). By using short-read sequencing, 80 *Arabidopsis* strains have already been sequenced with enough depth to provide an average of 6 to 12 reads for each nucleotide in the genome, and promising results have been obtained by identifying both induced and spontaneous mutations. The previous elucidation of the partial sequence of 20 *Arabidopsis* accessions by the Weigel group allowed the construction of a microarray chip that queries 250,000 single-nucleotide polymorphisms (Clark *et al*, 2007). This chip is being used by M. Nordborg (Los Angeles, CA, USA) to genotype 1,300 natural accessions, emphasizing the importance of this *Arabidopsis* sequencing project. The association mapping of 96 genotyped accessions and 101 different phenotypes has allowed an unprecedented resolution for some traits; the full 1,300 should increase mapping power and help to overcome complications from population structure. This microarray slide also opens many more opportunities; J. Borevitz (Chicago, IL, USA) proposed its use in assaying allele-specific expression levels, determining methylation patterns, alternative splicing analyses and expression quantitative trait locus (QTL) studies.

The symposium also illustrated that information gathering in the field—such as micro-meteorological observations—and the study of plant genetic diversity, fitness and performance, are crucial to understanding the mechanisms of adaptation to different environments. Contrary to other genetic systems, the lack of mobility in plants allows hypotheses on adaptation to be more easily tested, which—in combination with the current advances in genomics and the ease of genetic manipulation in *Arabidopsis* and other plants—provides a fantastic opportunity for studying the molecular nature of adaptation, and interactions between genotype and environment. Some presentations at the symposium focused on this emerging field of ecological genetics by analysing the responses of specific genotypes in diverse changing and natural environments, in contrast to the constant conditions used by most researchers. For example, Borevitz programmed growth chambers to mimic the photoperiod, temperature, light intensity and humidity in Sweden and Spain, and phenotyped *Arabidopsis* segregating populations and accessions, finding QTLs and associations exclusive to particular (simulated) locales (Li *et al*, 2006). E. Holub (Warwick, UK) is studying long-term recurrent populations of *Arabidopsis*. Focusing on pathogen response, he is characterizing the diversity and distribution of candidate disease-resistance genes across geographic and genomic contexts (Holub, 2007). J. Schmitt and A. Wilczek (Providence, RI, USA) coordinated an exciting project in which *Arabidopsis* populations and mutants with known laboratory phenotypes were planted across a matrix of sowing times and locations (Wilczek *et al*, 2009). An analysis of plants in the field instead of the laboratory revealed unexpected environmental responses from many known mutants, highlighting the importance of field studies.

Information transfer

There was particular excitement at the symposium about the transfer of information from model organisms to other species. J. Irwin (Norwich, UK) is characterizing variation in flowering time and vernalization requirements in *Brassica oleracea*, a species in which flowering time is an important determinant of harvestable tissue. Crosses and field trials are underway to use the *Arabidopsis* vernalization pathway to understand *Brassica* variants and to increase yield. Crop improvement could also potentially be achieved by the optimization of circadian pathways to elevate energy conversion rates. With this idea in mind, C.R. McClung (Hanover, NH, USA) showed promising preliminary results using video recordings of leaf movement to determine the variation of circadian rhythms in *B. rapa* accessions and recombinant inbred-line populations. To perform solid research in these new systems, successful high-throughput techniques must also be transferred from model systems to field crops. McClung has developed transformation methods for *B. rapa* calli that allow the monitoring of gene expression using a luciferase-based reporter, and has shown that shoots regenerated from *B. rapa* calli that overexpress the *Arabidopsis* circadian clock genes *TOC1* and *ZTL* have altered circadian rhythms.

One could say that the level of mechanistic understanding achieved in model species raises more questions that it answers. Are the crucial components implicated in environmental sensing and responses conserved across all plants? Is their function similar? The diversity of strategies and phenotypes is certainly enormous; however, in many cases the individual proteins are shared. Those attending the symposium realized this during the keynote address by W. Briggs, who reported on the notable diversity of LOV domain proteins in nature. Briggs and his collaborators G. Paris (Buenos Aires, Argentina), F. Goldbaum (Buenos Aires, Argentina) and R. Bogomolni (Santa Cruz, CA, USA) are studying LOV proteins in the pathogenic bacterium *Brucella*, and have found that infectivity is enhanced by blue light and LOV function (Swartz *et al*, 2007), emphasizing the

influence that research in plant species can have in opening new research fields in different domains of life. More examples of diversity in well-known genes come from the study of flowering time in perennial plants. In the annual *Arabidopsis*, 'winter-annual' ecotypes need to be exposed to long periods of cold before the longer days of spring can induce flowering. The repression of flowering is largely due to *FLC*, the expression of which is reduced during cold treatment. In addition, epigenetic modifications are acquired in the *FLC* locus that maintain low levels of expression after cold exposure, thereby allowing photoperiodic induction (Amasino, 2005). Perennials such as *Arabis alpina*—a close relative of *Arabidopsis*—flower repeatedly year after year, and are being studied by G. Coupland (Cologne, Germany). Coupland presented a genetic screen for *A. alpina* mutants that flower without vernalization, which led to the identification of *PEP1* as the *A. alpina* orthologue of *FLC* (Wang *et al*, 2009). The characterization of *PEP1* showed that, unlike for *Arabidopsis FLC*, epigenetic down-regulation is not maintained after vernalization, ensuring vegetative growth at some apices and promoting the perennial life cycle.

Finding homologous genes that have evolved new functions to promote different environmental responses across species was a recurrent feature discussed at the meeting. An example can be found in the *Populus* genus, which contains poplar, aspen and cottonwood trees. The relatively close phylogenetic relationship of this genus to *Arabidopsis*, coupled with the release of the whole genome sequence of the black cottonwood *Populus trichocarpa* (Djerbi *et al*, 2005), aid this type of research. O. Nilsson (Umeå, Sweden) has taken advantage of these tools to explore, in aspen trees, the role of photoperiodic flowering genes originally discovered in *Arabidopsis*. The *Arabidopsis* flowering-time gene *FT* acts as a florigen, moving from leaves to the meristems to promote flowering after photoperiodic induction (Corbesier *et al*, 2007). In aspen trees, bud set in preparation for winter is also photoperiodic and FT has a role in its regulation (Bohlenius *et al*, 2006). Surprisingly, FT is also involved in the temperature regulation of spring bud flush. In *Arabidopsis*, *FT* expression is induced by the CO protein, which only accumulates during long days when high levels of *CO* messenger RNA—regulated by the clock through GI—coincide with the perception of light (Sawa *et al*, 2007; Yanovsky & Kay, 2003). Nilsson assigned further evolutionary importance to the circadian regulation of CO by GI in aspen, by showing a latitudinal cline in the phase of oscillation of CO, which is at least partly due to the differential regulation of GI in these trees. The modulation of the CO phase allows FT expression to peak at different times of the year in trees from different latitudes, promoting flowering and bud set under the optimal environmental conditions at each location.

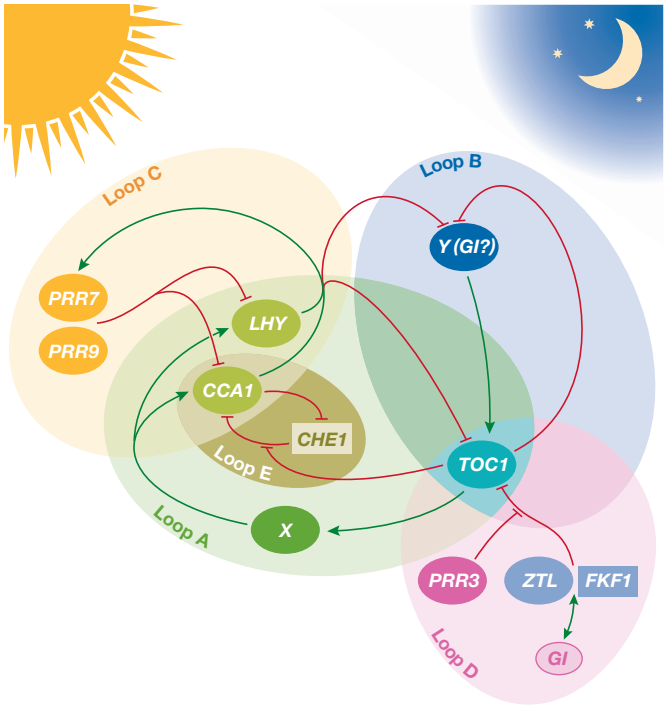

Fig 2 | Model of the *Arabidopsis* circadian clock. The circadian oscillator consists of a series of interlocking feedback loops (A–E). Genes newly reported to function in the clock are shown within rectangles. Loop A represents the transcriptional feedback loop that was identified initially and contains the morning-phased transcription factors *CCA1* and *LHY*, which negatively regulate *TOC1*. Component X, the existence of which has been inferred from mathematical modelling, induces the transcription of *CCA1* and *LHY*. *CHE1* could provide some of the functionality represented by X. Two evening-phased genes, *TOC1* and the yet-unidentified component Y, make up loop B. Morning-phased *PRR7*, *PRR9*, *CCA1* and *LHY* make up loop C. As reported at the meeting, *FKF1* works with *ZTL* to regulate *TOC1* negatively, and this process is, in turn, regulated by *GI* and *PRR3*, thereby constituting loop D. The existence of loop E, which provides a link between *TOC1* and *CCA1*, was proposed for the first time at the meeting. Some genes implicated in clock function have been omitted for clarity. Adapted, with permission, from Harmer (2009). CCA1, CIRCADIAN CLOCK-ASSOCIATED 1; CHE1, CCA1 HIKING EXPEDITION 1; FKF1, FLAVIN-BINDING KELCH REPEAT, F-BOX 1; GI, GIGANTEA; LHY, LATE ELONGATED HYPOCOTYL; PRR, PSEUDORESPONSE REGULATOR; TOC1, TIMING OF CAB EXPRESSION 1; ZTL, ZEITLUPE.

Mathematical modelling

The use of new technologies is spurring the development of faster and more-efficient algorithms to process and interpret data. The development of new methods that combine the various types of information available is also crucial to building new hypotheses. J.M. Maloof (Davis, CA, USA) illustrated how novel data mining can help to determine the gene underlying a QTL—typically a labour-intensive process. In this case, network analysis was used to combine publicly available genome resequencing, microarray expression and gene-annotation databases to identify a gene responsible for a QTL that affects the acceleration of flowering in response to foliar shade.

An exciting field is the development of mathematical models that integrate the information on well-studied processes gathered by molecular biologists, which is possible in organisms for which abundant data can be readily obtained or compiled. These models not only reproduce what has been observed but also predict how pathways and organisms will respond to future perturbations. In this regard, A. Millar (Edinburgh, Scotland) presented the latest analysis of an *Arabidopsis* circadian clock model that yields quantitative and dynamic predictions that are difficult to obtain from experimental data (Locke *et al*, 2006). Millar's model is able to reproduce the changes in clock phase that occur in response to the changing times of dawn and dusk through the year. This model predicted that changes in the entrainment of the clock must be accompanied by quantitative changes in the timing of clock gene

expression, which were subsequently confirmed experimentally. In addition, according to the model, the phase of *TOC1* expression is controlled by light input into the evening loop of the clock. New mathematical analysis aimed to test how such timing changes could be manipulated; counter-intuitively, changing light input into the morning loop of the clock was most effective in altering the photoperiod response of the evening loop. Planned and spontaneous presentations at the meeting illustrated the importance of the interactions between 'wet bench' and computational approaches. Millar found that the clock he modelled was resistant to resetting by pulses of TOC1, as Tobin had previously found for the real clock. CHE1, which was described by Kay, could represent part of the component 'X' predicted by modelling. Finally, the modification of the parameters of the Millar clock model allowed H. Nimmo (Glasgow, UK) to validate his recent observation of a modified root clock, which is a version of the clock that has no light input, and in which the morning loop proteins CCA1 and LHY do not bind to the promoters of the evening loop genes (James *et al*, 2008).

Also remarkable is the model put forward by J. Schmitt (Manhattan, KS, USA), which was developed in collaboration with S. Welch (Manhattan, KS, USA) using the field-collected data on *Arabidopsis* flowering-time mutants discussed above (Wilczek *et al*, 2009). This model calculated the timing of bolting as a function of accumulated temperature, photoperiod and vernalization exposure, reproduced the observed data and, importantly, predicted unexpectedly sharp transitions from rapid cycling to winter annual life histories depending on germination date—a prediction that was subsequently verified experimentally.

Summary

This is a truly remarkable time to be studying plant environmental sensing and response. Understanding and manipulating these responses will be crucial for maintaining agricultural productivity and conserving biodiversity in the face of increasing climate change. The symposium showed that research in these areas is moving at a rapid pace, fuelled by fundamental discoveries in model organisms, and the increasing availability of high-throughput technology in model and non-model systems alike.

ACKNOWLEDGEMENTS

We thank S. Harmer for helpful discussion and for providing the template for Fig 2. Work in the Maloof laboratory is funded by National Science Foundation grant DBI-0820854.

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