Light responses of a plastic plant

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***Arabidopsis thaliana* isolates from the wild vary enormously in their morphology and physiological responses to standard conditions, indicating that substantial genetic variation is accessible in this species. Natural variant alleles encoding two *Arabidopsis* photoreceptors, phytochrome A and cryptochrome 2, have now been identified by different experimental methods. The amino-acid substitutions suggest new features of phytochrome and cryptochrome function that regulate plant growth and flowering time.**

Geneticists often concentrate on standard strains of a model species. Many groups working on *Arabidopsis thaliana* are now looking anew at the natural diversity of this model plant. The commonly used *Arabidopsis* strains were selected for very short life cycles, for example, whereas many natural isolates ('accessions') are winter annuals that take much longer to flower. The plasticity of *Arabidopsis* development was clear to the earliest investigators, who noted many differences in vegetative growth between accessions. Seed collections started a half-century ago are now house accessions isolated anywhere from the sub-tropics to the borders of the Arctic. Can the genetic basis of their natural variation be determined? If so, how, and what will we learn about plant development? The causes of flowering-time variation were among the first to be tackled, revealing that genes involved in the cold response were weakly expressed or mutated to inactivity in some accessions[1,2]. On pages 435 and 441 of this issue, Salah El-Din El-Assal and colleagues[3] and Julin Maloof and colleagues[4] report studies of natural variation in photoreceptor genes (Fig. 1) and, in so doing, provide intriguing clues to the molecular mechanisms of environmental response pathways.

Photoreceptor diversity

Phytochrome and cryptochrome photoreceptors control development from seed germination, through seedling growth, to the shape and the pigmentation of mature rosette leaves, to flowering time. The five phytochromes, encoded by the genes *PHYA–PHYE*, respond to red and far-red light[5], whereas the cryptochromes, encoded by *CRY1* and *CRY2*, respond to blue and UV-A wavelengths[6]. The first natural variant, a small deletion in the *PHYD* coding region of the Ws accession, was found serendipitously[7]. As *PHYA* and *PHYB* have the dominant functions among the five *PHY* genes, the *PHYD-Ws*–null allele caused only minor phenotypic changes.

The two groups describing their work in this issue take alternative, directed approaches to identify natural variation. El-Assal *et al.*[3] have studied intensively a single accession from the Cape Verde Islands (Cvi), a habitat that differs widely from that of the standard lab strains. Recombinant inbred lines (RILs) were created by crossing Cvi to Landsberg *erecta* (a lab strain originating in
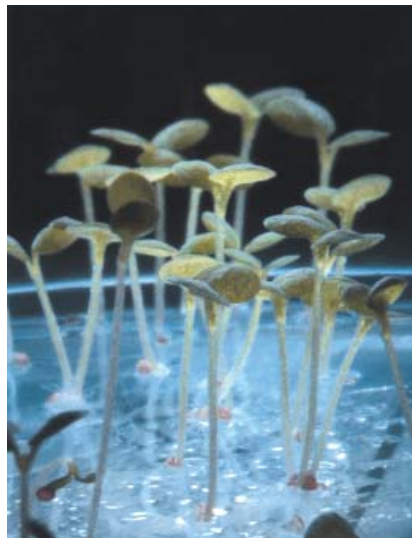

Fig. 1 Garden-variety genetics. *Arabidopsis* seedlings (7d) are shown. Wide genetic variation in light response is seen among *Arabidopsis* accessions both for flowering time traits[3] and for hypocotyl length[4]. Photo courtesy of Detlef Weigel.

Northern Europe), breeding 162 recombinants for 8 generations and mapping their genomes. Phenotypic studies revealed a wide range of flowering times among the RILs, and the underlying genes were mapped to four chromosomal regions by using quantitative-trait locus (QTL) analysis[8]. El-Assal *et al.*[3] now map the major, early-flowering QTL more finely, to 1 of 12 base changes in the Cvi allele of *CRY2* (Fig. 2).

Maloof *et al.*[4], in contrast, start from a phenotypic survey of 140 accessions for seedling growth under four light

conditions. They follow up directly with molecular analysis of candidate genes and proteins in the accessions at the extremes of the response range, without genetic mapping. The growth of the seedling hypocotyl under far-red light was known to be controlled by only one photoreceptor gene, *PHYA*. It is very satisfying that the Lm-2 accession (one of the accessions under study), which was 100-fold less sensitive to far-red light than lab strains, turns out to be defective in *PHYA* function (Fig. 2)[4].

The RIL approach takes time but creates an 'immortal' resource. QTL analysis can then detect gene interactions and subtle phenotypic effects[9]. Several groups are using these RILs to map other QTL. The ecotype survey carried out by Maloof *et al.*[4] is useful only for the trait that is initially surveyed, and then concentrates upon the effects of known candidate genes. In the future, we can expect QTL analysis to follow surveys, using recombinants between the extreme accessions. The reports by El-Allal *et al.*[3] and Maloof *et al.*[4] motivate such efforts because natural variants led both groups to new biology.

Night and day

Most *Arabidopsis* accessions flower rapidly when plants are grown in light:dark cycles with a long day and a short night, and more slowly under short-day cycles. CRY2 protein is abundant at all times in a long-day cycle and *CRY2-Cvi* had little effect upon flowering time or the levels of CRY2 in these conditions. Most unexpectedly, El-Assal *et al.*[3] found that in short-day cycles, CRY2 is rapidly degraded in response to light and only re-accumulates at night. CRY2 abundance at the end of the day is thus a molecular indicator of photoperiod. CRY2-Cvi remains abundant in short-day conditions, obscuring the photoperiod signal and leading to the early flowering of *CRY2-Cvi* plants[3].

The biochemical mechanism that leads to the far-red insensitivity of *PHYA-Lm-2* is equally intriguing. The single amino-acid change is located in the hinge region
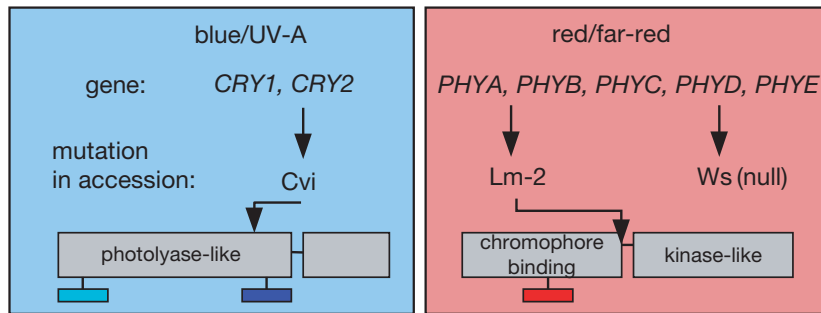
Fig. 2 Natural variation in *Arabidopsis* photoreceptor genes. The approximate positions of the relevant amino-acid changes in the photoreceptor proteins is indicated, relative to the chromophores (rectangles, colors indicate the wavelengths absorbed). The cry2 photoreceptor from Cvi is more stable in short days; the phyA photoreceptor from Lm-2 is 100-fold less responsive to far-red light. The chromophore-binding domain of cryptochromes has sequence similarity to type II DNA photolyases.

of phytochrome, between the better-studied chromophore-binding and protein kinase domains (Fig. 2). PHYA is normally light-labile, yet surprisingly PHYA-Lm-2 accumulates equally in the light as it does in darkness[4]. Subtle changes in the autophosphorylation efficiency and in the absorption spectrum of a reconstructed PHYA-Lm-2 protein[4] do not obviously account for the phenotype. The hinge domain is clearly important for phytochrome function: light-sensitivity of PHYB is also greatly reduced by the amino-acid change equivalent to *PHYA-Lm-2* (ref. 4), and another mutation in this region has previously been shown to result in increased light sensitivity[10].

The power of nature

Whatever biochemistry remains to be unraveled, these papers render a clear judgement on the value of studying natural genetic variation in *Arabidopsis*. Natural variation can affect the critical photoreceptors, disposing of the view that only minor, modifier genes would be identified because mutations in the important genes would have been selected against. The natural alleles are not simply alterations in expression level or null alleles but include highly informative amino-acid substitutions. These can have striking phenotypes, not always the ineffable subtleties that give QTL a reputation for being hard to study. Natural variation in light response pathways might prove to be particularly rich, but they are not exceptional, as the variation for flowering time shows, so the plastic development of *Arabidopsis* accessions is likely to offer up many other insights into plant physiology. Ultimately, studies of natural genetic variation should lead to a better understanding of natural selection[9]. *Arabidopsis* has some promise in this area, which will be realized as more representative samples are collected from natural populations, accompanied by better information on their habitats. □

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