

few would have expected. The predicted chromatic adaptation sensor RcaE indeed contains the four C-terminal motifs expected for a histidine sensor kinase, including the histidine itself. However, the N-terminal domain contains a region with similarity to a known chromophore attachment domain – that of phytochrome. Homology between phytochrome and bacterial sensor kinases was previously predicted, from sequence comparison alone, by Schneider-Poetsch⁸, but a weak link in the argument was replacement of the histidine autophosphorylation site by the tyrosine of phytochrome. With RcaE (Ref. 5), the homology with phytochrome is undeniable, and the histidine is conserved. Furthermore, two-component regulation came to light in eukaryotes in 1994 (Ref. 9), with the sequences of an ethylene-response element from *Arabidopsis* and of another, unspecified receptor, from *Saccharomyces*. Intriguingly, RcaE also shows similarities to the plant ethylene-response element⁹.

It is too early to expect detailed biochemical analysis, but it must soon follow. There are certainly cyanobacterial phosphoproteins^{10,11} and two-component systems^{12–14}. What is the RcaE chromophore? RcaE lacks the cysteines that ligate the linear tetrapyrrole chromophore of phytochrome. Perhaps RcaE itself has no chromophore, and is a photosensor controlled by a photoreceptor, analogous to the chemoreceptor and chemotaxis sensor and response regulators of *E. coli*. The phycoerythrin and phycoerythrin chromophores themselves are also linear tetrapyrroles. It is tempting to think that the evolutionary prototype of the photoreceptor phytochrome was itself a photosynthetic light-harvesting protein, capable of regulating its own synthesis. While red light repression of phycoerythrin synthesis may well be explained by the phytochrome-like properties of RcaE, the green light activation of phycoerythrin synthesis occurs over a spectral range outside of the response of phytochrome. It remains to be seen whether the biliprotein spectral window is modified in the photoreceptor, or whether another photosensory system, for which the rhodopsins are especially suited, is responsible for effects of green light.

Other responses to spectral composition

Complementary chromatic adaptation is not the only way in which cyanobacteria sense their light environment – indeed, many species do not exhibit the phenomenon at all. A more widespread, long-term response to altered spectral composition is adjustment of the stoichiometry of photosystem I and photosystem II of the photosynthetic electron transport chain¹⁵. Again, the response is complementary to the change in the light regime: photosystem I absorbs more at higher wavelengths than photosystem II, and becomes relatively more abundant under blue-green illumination, as if to make good by sheer quantity its limited light-

harvesting capacity. As a function of light intensity, too, the ratio of photosystem I to photosystem II changes – from near to unity in saturating light to a sixfold increase in favour of photosystem I in low light.

Short-term adaptations – state transitions – also satisfy the need to balance photosystem I with photosystem II. State transitions involve post-translational, covalent modification of pre-existing proteins, most clearly in chloroplasts, where the functional equivalent of the cyanobacterial phycobilisome is the major light-harvesting chlorophyll–protein LHC II. LHC II becomes phosphorylated, catalysed by a protein kinase whose activity is regulated by the redox state of electron carriers located between photosystem I and photosystem II (Ref. 10). Phospho-LHC II, produced in response to a redox signal to the LHC II kinase, moves from photosystem II to photosystem I, restoring balanced delivery of light energy to the two photosystems¹⁰. Cyanobacteria and red algae also perform state transitions, with a mobile phycobilisome responding to the redox state of electron carriers located between the two photosystems¹⁰. However, phycobilisome-based state transitions are unlikely to be driven by the same sort of kinase as that found in chloroplasts¹⁶. The chloroplast LHC II kinase itself is much sought, but has proved elusive. Recent evidence suggests a location in the core of photosystem II (Ref. 17).

In photosynthetic organisms, redox control means light control. The underlying mechanism of adjustment of photosystem stoichiometry probably involves redox control, rather than direct photocontrol, of gene expression^{10,15,18,19}. The universal eukaryotic location of the genes for the core components of the two photosystems in chloroplasts rather than in the nucleus immediately suggests a reason for the maintenance of the extranuclear genomes of chloroplasts (and, by analogy, mitochondria): electron transport holds a tight rein on the expression of genes for its own components^{3,20}.

Cyanobacterial phytochrome

For research on cyanobacteria, and indeed biology as a whole, an important development was the completion in 1996 of genome sequencing of *Synechocystis* PCC 6803 (Ref. 21). It seems to have taken 24 people under two years to obtain the complete sequence of approximately 3.5 Mb. Thanks to the openness and generosity of the participants, the question 'is there a cyanobacterial gene with homology to x?' can be addressed immediately using the CyanoBase site on the World Wide Web (<http://www.kazusa.or.jp/cyano/>).

Synechocystis 6803 is not a complementary chromatic adapter. However, using CyanoBase, *Synechocystis* PCC 6803 appears to contain several histidine sensor kinases with homology to phytochrome. Perhaps colour of light does other things through two-component signal transduction, such as triggering development (this is

known in other species¹⁴). Or maybe the photosystem stoichiometry and state transition redox sensor(s) are there at the origin of photomorphogenesis. Furthermore, *Synechocystis* PCC 6803 contains a gene, *slr0473*, the predicted product of which has 36% identity to that of the *phyC* gene product of *Arabidopsis*: cyanobacteria have no seed dormancy, no photoperiodism and no phototropism, but they certainly contain phytochrome. Unexpected certainty is unusual in science, but a complete genome sequence can give precisely that. And what would Stanier¹ have thought of CyanoBase?

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