and mating systems are more likely than others to tip the scales in favour of cooperation. In particular, both polygyny [12] and overlap between generations [13] tend to boost the evolution of altruistic behaviour. Indeed, these traits even allow for altruistic acts directed towards random group members, without a need for kin recognition. These results suggest that the lifestyle of the greater horseshoe bat may be especially conducive to cooperative behaviour based on kin selection. There is only one problem: there is, thus far, no evidence that greater horseshoe bats engage in such behaviour despite many years of research on this species.

In other bats, several cooperative behaviours have been described. They range from feeding starved colony members [14], to nursing foreign pups [15], to information transfer about food [16] and suitable roosts [17]. Remarkably, most of these cooperative behaviours are apparently not preferentially directed towards kin. Blood regurgitation in vampire bats is even one of the few possible cases of reciprocal altruism in wild animals. Moreover, in the few bat species for which relevant data are available, relatedness does not explain spatial associations of individual females within colonies [18]. In greater horseshoe bats, however, no cooperative behaviours have been described and the only kin-directed behaviour shown — daughters sharing foraging areas with their mothers [19] — cannot be used to explain benefits due to increased relatedness within matrilines. Therefore, our current knowledge of bat sociobiology does not suggest that kin selection is the most important factor for stabilizing bat colonies [20]. In fact, if entire colonies function as social units, higher relatedness within matrilines and hence greater genetic differentiation between matrilines, as observed in greater horseshoe bats [2], may even disrupt social groups when cooperation would be directed towards kin only.

To determine the importance of mate sharing between relatives for kin selected cooperation and group stability we have to look at mate choice in animals where females live in groups consisting of several matrilines and that show cooperation. The current lack of evidence for cooperation among horseshoe bats does ask for a closer look at the social behaviour of this species. However, it should be kept in mind that even in taxa with high levels of relatedness among group members, such as in clonal aphids or haplo-diploid insects, cooperation is the exception rather than the rule [4].

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DOI: 10.1016/j.cub.2005.10.059

Photosynthesis: The Processing of Redox Signals in Chloroplasts

Recent work identifies two kinases required for phosphorylation of proteins of chloroplast thylakoid membranes. One kinase, STN7, is required for phosphorylation of light-harvesting complex II; another, STN8, is required for phosphorylation of photosystem II. How do these kinases interact, what do they do, and what are they for?

John F. Allen

Phosphorylation of chloroplast proteins was first reported in 1977, and shown to be light-dependent [1]. The implications of this landmark discovery are still being worked out. Now that mutants are available for a protein kinase whose activity was first demonstrated by John Bennett [1], one story can be retold with increased confidence. But there are clearly multiple chloroplast kinases, with multiple substrates and multiple effects. This was forecast [2], but only recently has a second protein kinase been identified, putting the phenomenon of chloroplast protein phosphorylation on course for more complete biochemical

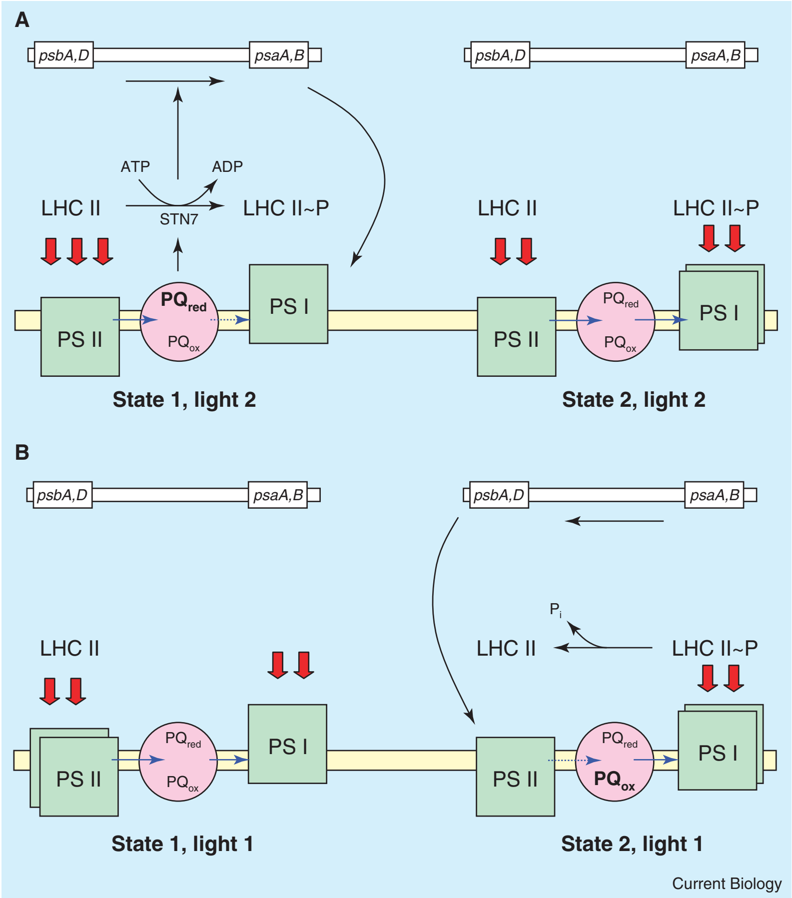

Figure 1. State transitions and control of gene expression in chloroplasts.

Proposed action of the LHC II kinase and transcriptional regulator STN7 during state transitions and adjustment of photosystem stoichiometry by means of transcriptional control of *psaA,B* (photosystem I) and *psbA,D* (photosystem II) reaction centre genes. If plastoquinone (PQ) becomes reduced (A, left) there are two consequences — activation of the STN7 LHC II kinase, and a relative increase in photosystem I (PS I) gene transcription. If plastoquinone becomes oxidised (B, right) then LHC II becomes dephosphorylated, and there is a relative increase in photosystem II (PS II) gene transcription.

investigation. There are provisional reports of further chloroplast kinases and phosphatases: two is certainly not enough. The final number of chloroplast kinases can only be guessed, so the story is likely to become more complex. Here I will argue that we are now catching glimpses of what will be resolved, eventually, as a redox signal-processing unit, a self-adjusting device which incorporates the chloroplast genetic apparatus, in addition to a network of post-translational modifications of pre-existing proteins.

To start with what can still be said: one of the chloroplast protein phosphorylation reactions, acting on apoproteins of the pigment-containing light-harvesting complex II (LHC II), is activated when plastoquinone, an electron carrier, is reduced. This redox-controlled reaction now has a well-characterised role in the regulation of photosynthesis — it serves to distribute absorbed excitation energy optimally between chloroplast photosystems I and II [3]. This means that plants and algae are able to make the best use of the available light energy by continuously monitoring the relative rates of electron transport through the reaction centres of the two photosystems.

For maximal efficiency and safety of operation, the reaction centres should remain balanced in their rates of light energy conversion and light-driven electron transport. If they become unbalanced — for example by a change in spectral composition of light which favours one photosystem over the other — then plastoquinone changes its redox state. It does this simply because plastoquinone accepts electrons from photosystem II, and donates them to photosystem I. When the photosystems are balanced, the rate of electron flow into plastoquinone will equal the rate of electron flow out. When photosytem II runs momentarily faster than photosystem I, plastoquinone becomes reduced, the LHC II kinase is activated, and phosphorylated LHC II, with its light-absorbing chlorophylls, moves from photosystem II to photosystem I, making good the imbalance of light harvesting that delivered surplus energy to photosystem II, where it was wasted, as fluorescence or heat.

Conversely, if photosystem I receives more than its usable share of available light energy, plastoquinone becomes oxidised, the kinase becomes inactive, and a phospho-LHC II phosphatase acts to restore unphosphorylated LHC II, with its chlorophyll molecules, to photosystem II. In essence, this biochemical explanation of ‘state transitions’ — the adaptive, complementary alteration of the light-harvesting capacity of the photosystems — was mapped out in the 1980s [2]. Besides characterisation of the LHC II kinase and phosphatase, there are at least two important directions for the future. What, actually, happens to LHC II as a result of its phosphorylation? Why, and how, does reaction centre chloroplast gene transcription provide a parallel means of balancing the two photosystems in response to the redox signal from plastoquinone?

Other than LHC II, which serves both photosystems, protein substrates of chloroplast thylakoid membranes seem to be mostly components of photosystem II, including the ‘D1’ product of the chloroplast *psbA* gene, at the core of the photosystem II reaction centre. Another conspicuous phosphoprotein was described by Bennett [1] as simply “the 9 kDa phosphoprotein”. This turns out to