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From light to life: an interdisciplinary journey into photosynthetic activity

Workshop on Molecular Genetics and Biophysical Aspects of Photosynthesis

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On the snowy slopes of Les Diablerets, some skiers seemed to be outlining the Z-scheme of photosynthetic electron flow: up the PSII chair lift to Les Mazots, down the b_6f trail and up the PSI chair lift to the summit at Meilleret. Others were depicting cyclic flow by repeatedly riding the PSI lift to Meilleret and returning to its base via the b_6f trail. But the flow of skiers did not generate a proton gradient, and if any energy was captured it was in the form of renewed enthusiasm to attend the sessions of the EMBO workshop entitled: 'Molecular Genetics and Biophysical Aspects of Photosynthesis', which was organized by J.-D. Rochaix, W. Rutherford and F.-A. Wollman and took place from 26 to 29 January 2003.

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Introduction

One intention of the organizers of the EMBO workshop on Molecular Genetics and Biophysical Aspects of Photosynthesis was to bring together scientists with different backgrounds and experimental approaches. Indeed, the meeting proved that photosynthesis is a privileged field of interdisciplinary research, in which each of the many methods used in its investigation (whether biophysical, biochemical or biological) provides measurements on a timescale appropriate to the vastly different turnover rates for the process it investigates. As pointed out in one of the opening lectures by L. Mets (Chicago, IL, USA), these can vary in range from fractions of picoseconds for the energy transfer between the chlorophylls in the light-harvesting antennae to days or years for growth and development. Genetic analysis stood out at the meeting because, in synergy with other approaches, it contributes to our understanding across a vast range of these timescales. Indeed, the analysis of mutant phenotypes was a recurrent theme throughout the meeting (a typical example is shown in Fig. 1).

Assembly and maintenance of the photosynthetic machinery

Making and maintaining the plastid requires the import of thousands of nucleus-encoded polypeptides (Fig. 2). S. Baginsky (Zürich, Switzerland) warned that in his extensive proteomic survey of plastid proteins, ~40% were not predicted by the commonly used algorithms to be imported into the plastid. This implies that the plastid proteome may be significantly larger than previously estimated.

Protein translocation into the chloroplast is known to be mediated by the Toc and Tic complexes in its outer and inner envelope membranes, respectively. Toc159 and Toc34 are GTP-binding proteins that also bind precursor polypeptides; Toc75 forms the membrane pore and Toc64 is involved in the docking of precursors to the membrane. J. Soll (Munich, Germany) reported that Toc75 and Toc159 are sufficient to allow GTP-dependent polypeptide import when they are reconstituted into liposomes. He suggested that the energy from GTP hydrolysis might allow Toc159 to drive the import of the polypeptide precursor through the Toc75 pore. F. Kessler (Neuchâtel, Switzerland) showed that the Toc159 protein is localized in the outer envelope, as expected, but is also present at similar levels in the cytosol, as a soluble protein. Furthermore, a Toc159 mutant polypeptide that does not bind or hydrolyse GTP localized only to the cytosol in

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Arabidopsis, and failed to integrate into the envelope *in vitro*. Thus, a GTP-hydrolysis/GDP-exchange cycle may regulate the insertion of Toc159 into the chloroplast envelope.

Over the course of evolution, specialized photosynthetic membranes, the thylakoids, appeared at the same time as the emergence of oxygenic photosynthesis. J. Soll showed that treatment with inhibitors of vesicular membrane fusion leads to the accumulation of vesicles in the chloroplasts of land plants. This suggests that plastids have evolved a vesicular mode of thylakoid membrane biogenesis. As endosymbiotic descendants of a prokaryote, plastids may have acquired this pathway from their original eukaryotic host. The cargo of these vesicles might include some of the proteins that are directed to the thylakoid membrane or to its lumen, as well as lipids, pigments and pigment precursors.

The vast majority of chloroplast proteins are encoded by nuclear genes, including the factors involved in chloroplast gene expression. In plants and algae, mutational analyses have revealed that the products of a surprisingly large class of nuclear genes are required for the post-transcriptional steps of plastid gene expression, including: RNA processing, RNA splicing, RNA turnover, translation, protein assembly and degradation (M. Goldschmidt-Clermont, Geneva, Switzerland; W. Gruissem, Zürich, Switzerland; P. Westhoff, Düsseldorf, Germany).

In the green alga *Chlamydomonas reinhardtii*, the translation of cytf (a subunit of the cytochrome b_6f complex; Fig. 3), is repressed by the low levels of unassembled cytf that accumulate when other subunits of the complex are missing (Choquet *et al*., 2001). This is in contrast with the fate of other subunits, which are rapidly degraded when unassembled. Y. Choquet (Paris, France) presented evidence that similar negative-feedback loops may also regulate the translation of specific subunits from all the other photosynthetic complexes. This homeostatic regulation may be important because it maintains constant pools of these subunits, which might be important for the assembly of the others.

The photosystems (PSI and PSII) are complexes of proteins and pigments that convert light into redox potential through a photochemical reaction. This process occurs in a specialized structure, the reaction centre. The photosystems contain proteins that absorb light (the inner antennae), and are surrounded by many light-harvesting complexes (LHCs), which form the outer antennae. The assembly of these complex structures is a dynamic process, as described for PSII by E.-M. Aro (Turku, Finland). By using protein pulse-labelling followed by two-dimensional electrophoresis to analyse chloroplast mutants of tobacco, she showed that the small PSII subunit PsbL is essential for the stable association of the CP43 subunit with PSII monomers, whereas PsbJ is required for the formation of the PSII–LHCII supercomplexes.

H. Scheller (Frederiksberg, Denmark) is using *Arabidopsis* to investigate the role of individual PSI subunits. Of particular interest are those that are found in plants and algae but not in cyanobacteria (PSI-G, -H, -N and -O), as the X-ray structure of PSI that is available at present was obtained from a cyanobacterium (see below). Electron fluxes through the photosystems are regulated by state transitions, a process in which LHCII migrates between PSII and PSI in response to phosphorylation (Fig. 3). Plants lacking PSI-O, -H or -L show reduced state transitions. The binding of PSI-O to the complex depends on both PSI-H and PSI-L. Crosslinking studies show that the three proteins are closely associated and that PSI-L can interact with the LHCII protein Lhcb1. Thus, these subunits may provide a docking site for phosphorylated LHCII on PSI, explaining their role in state transitions.

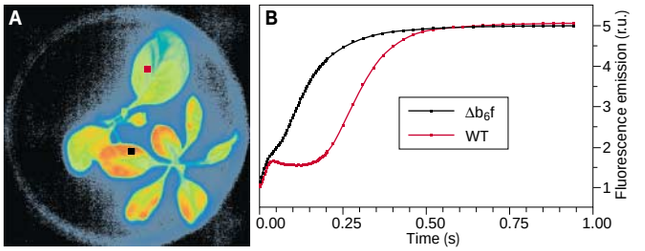

Fig. 1 | Chlorophyll fluorescence imaging of photosynthetic mutants. (**A**) Digital imaging of the fluorescence emitted by wild-type seedlings (WT; left) and a mutant plant that lacks the cytochrome b_6f complex (Δb_6f; right). (**B**) Kinetics of fluorescence emission measured at the points indicated in (A) by the red and black squares. The mutant was provided by D. Stern (Ithaca, NY, USA).

The harvesting of light for photochemistry is a dangerous business, and PSII pays a heavy toll in photodamage. As reviewed by I. Ohad (Jerusalem, Israel), damage occurs at all light intensities, and the primary victim is the PSII D1 subunit, which is rapidly degraded and replaced through an active repair cycle. An early step in the repair cycle is the cleavage of D1 on the lumenal side of the thylakoid membrane by an endoprotease, DegP2, to give a 23-kDa intermediate. Z. Adam (Rehovot, Israel) showed that this fragment is further degraded by FtsH, a membrane protease that faces the stroma, in a process that can be reconstituted *in vitro* using recombinant proteins. The genes that encode this protease belong to large families, with some members being expressed differently in response to light or other forms of stress. Members of the *FtsH* family in *Arabidopsis* may have partly redundant functions, as suggested by the lack of an obvious phenotype in an *FtsH1* mutant and the variegation in the leaves of *Arabidopsis FtsH2* and *FtsH5* mutants. By contrast, their orthologues in other species may be less redundant; P. Nixon (London, UK), reported that disruption of one of the *FtsH* genes in *Synechocystis* 6803 leads to increased light sensitivity and severely impaired repair of PSII in high-intensity light.

Apart from its role in photosynthesis, light also regulates many aspects of plant development and gene expression. Phytochromes are light-receptor protein kinases that are regulated by red and far-red light. Phytochrome-like proteins have also been found previously in prokaryotes, and A. Vermeglio (Cadarache, France) described a novel type that is found in *Rhodopseudomonas palustris* and in a symbiotic *Brahdyrhizobium* strain. The *BphP* gene encodes a phytochrome that has the familiar chromophore-binding domain and a PAS (Per/ARNT/Sim) domain, which is otherwise found only in eukaryotic phytochromes, but lacks a histidine-kinase domain. In this case, the light signal is transduced by the inhibitory protein–protein interaction of BphP with PpsR, which is itself a negative transcriptional regulator of photosynthetic genes in aerobic conditions.

Plants adapt not only to changes in light conditions, but also to many other aspects of their environment, and in particular to nutrient limitation. To systematically explore this type of adaptation, A. Grossman (Stanford, CA, USA) used microarrays of *Chlamydomonas* complementary DNAs. He showed that acclimatization to sulphur deprivation involves increases in the levels of many transcripts, for example those encoding proteins involved in sulphur scavenging and assimilation, and cell-wall proteins with particularly low sulphur contents, as well as decreases in other transcripts, such as those for PSII proteins. In *sulphur acclimation 1* (*sac1*), a regulatory

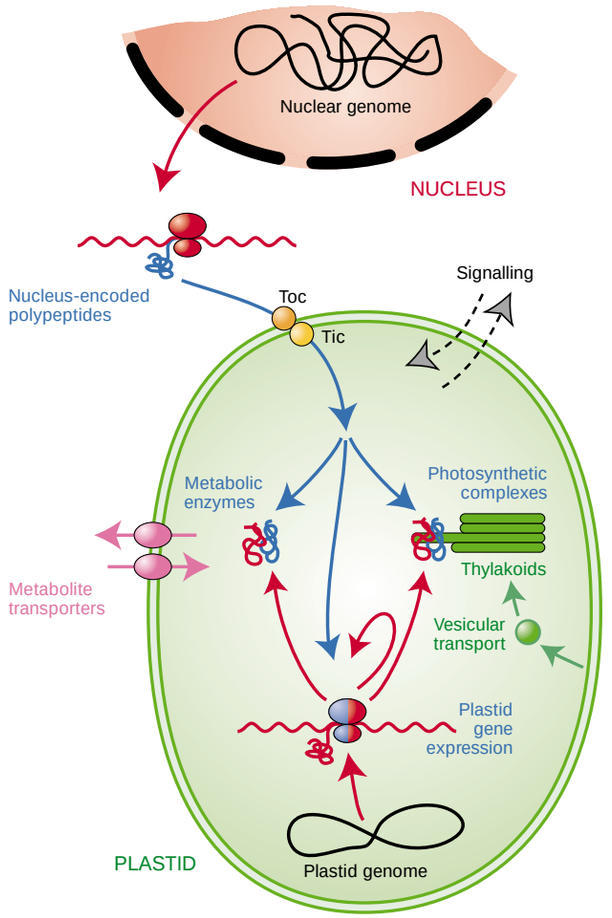

Fig. 2 | Plastid biogenesis. Many nucleus-encoded polypeptides are imported into the plastid through the translocons of the outer and inner chloroplast envelope membranes (Toc and Tic, respectively). Some of these polypeptides assemble with others that are encoded by plastid DNA to form photosynthetic complexes or metabolic enzymes. Many of the nucleus-encoded polypeptides also participate in various steps of plastid gene expression. The nucleocytosolic and plastidic compartments also exchange metabolites and regulatory signals. (Image drawn by Nicolas Roggli, University of Geneva, Switzerland.)

mutant that dies under conditions of sulphur stress, the levels of many (although not all) of these transcripts do not change. Thus, the Sac1 regulator governs part of the response, but is not the master regulator.

Under low copper conditions, *Chlamydomonas* cells respond by activating backup genes to replace copper-containing proteins through several different pathways. For example, plastocyanin is replaced by an iron-containing cytochrome as an electron carrier from the b_6f complex to PSI (Fig. 3). In addition, S. Merchant (Los Angeles, CA, USA) showed that for iron assimilation, the *Crd2* pathway is activated to bypass a copper-containing ferroxidase. Mutations in the genes for these surrogates lead to copper-conditional phenotypes. Merchant's group also identified a pair of homologous genes, *Crd1* and *Cth1*, that are reciprocally expressed under copper limitation versus repletion and encode oxygen-dependent di-iron enzymes. The reduced chlorophyll protein accumulation in *crd1* mutants in conditions of copper limitation was explained by the finding that Crd1 is involved in chlorophyll biosynthesis, consistent with an earlier proposal that its homologue in *Rubrivivax gelatinosus*, AcsF, is the elusive cyclic oxidative cyclase (C. Astier, Gif-sur-Yvette, France). It is puzzling that the *crd1* mutation specifically affects PSI and its antenna LHCI.

Iron limitation causes a dynamic adaptation of the protein composition of the thylakoid membrane. Using two-dimensional gel electrophoresis and mass-spectrometry, M. Hippler (Jena, Germany) was able to unravel part of the mechanism for the protein degradation that is involved in this process: degradation of the LHCI protein Lhca3 involves a specific amino-terminal cleavage.

Light harvesting

Light excitation is transferred from the antenna proteins to the reaction centres, where a strongly reducing species of the centre is formed and, consequently, an electron is transferred between a primary electron donor and an acceptor. Without detailed knowledge of the structure of the photosystems and their antenna partners, the evaluation of the energy-transfer parameters has usually been based on theoretical models that comprise an energy-transfer ('hopping') rate between two chlorophylls in the antenna and the intrinsic photochemical rate of the reaction centre. During the past decade, however, the atomic structures of the main photosynthetic complexes have become available, and femtosecond laser-spectroscopy has permitted the estimation of the rates of individual energy-transfer steps. These two breakthroughs have greatly enhanced our knowledge of light harvesting in photosynthetic organisms. On the basis of these approaches, R. van Grondelle (Amsterdam, The Netherlands) proposed a model for PSI in which the average time taken for a single energy-transfer step is ~150 fs and trapping requires ~8 ps.

R. Bassi (Marseille, France) investigated the ability of LHCII to dissipate excess light energy (photoprotection). Non-radiative dissipation in LHCII is modulated by changes in the carotenoid composition of the different LHC proteins that form this complex, with xanthophylls having a major role. Bassi showed that different binding sites have different affinities for carotenoids, and that stress conditions (mainly light and cold) affect their nature and number in the LHC proteins. Thus, carotenoid binding regulates the efficiency of light harvesting by allosteric modification of antenna protein conformation.

The peripheral (LH2) and core (LH1) antennae of photo synthetic bacteria are highly symmetrical structures compared with their plant counterparts, PSII/LHCII and PSI/LHCI. This is probably due, at least in part, to the sizes of their elementary building blocks, which in bacteria are small proteins that assemble into larger ring systems. No such symmetry is found for PSI, whose outer antenna (which is composed of LHCI dimers) is located on one side of the core. In PSII, an intermediate situation is found, as LHCII trimers display a perfect C3 symmetry. R. Cogdell (Glasgow, UK) discussed the question of the true oligomeric state of the bacterial LH antennae, pointing out that the integrity of the LH rings may be disrupted *in vivo*. He proposed that members of the PufX protein family could allow the passage of the membrane-soluble quinone through the LH rings that surround the reaction centre.

Reaction centres

The photochemical and photo-induced electron-transfer reactions that occur in the reaction centres (for a review, see Nicholls & Ferguson, 2002) have long been studied using both spectroscopic techniques and site-directed mutagenesis. This knowledge has now been advanced by the recent determination of the X-ray structures of PSI and PSII. P. Fromme (Temple, Arizona, USA) presented the structure of the PSI complex from the cyanobacterium *Synechococcus elongatus* at 2.5-Å resolution, clearly identifying the positions of the individual subunits and cofactors. She focused on the two phylloquinones, molecules that have been reported to be equally reduced on exposure to light, but are then reoxidized by the nearest [4Fe4S] cluster at rates that differ by almost one order of magnitude. She proposed that their different local environments could explain this difference. Indeed, two of the four structural lipids identified bind in close vicinity to the phylloquinones and are very different: one is a phosphatidyl glycerol and the other a monogalactosyl diacyl glycerol.

As a complementary approach to three-dimensional crystallography, P. Sétif (Saclay, France) showed that the interaction between PSI and a soluble electron carrier, ferredoxin (Fd), can be studied by site-directed mutagenesis. As well as confirming the electrostatic nature of their interaction, extensive mutagenesis of charged residues on both partners allowed Sétif to draw a detailed map of the Fd docking site on PSI.

A remarkable recent achievement is the determination by X-ray crystallography of the three-dimensional structure of PSII from the thermophilic cyanobacterium *S. elongatus* at 3.8-Å resolution. Fromme discussed how the recent refinement of the side-chain assignments made it possible to identify His 190 of the D1 polypeptide. Functional studies suggested a role of His 190 in the deprotonation that accompanies the oxidation of Y_Z, a D1 tyrosine residue that is part of the electron-transfer chain. However, the crystallographic data are incompatible with this role, as the distance between these two residues is not consistent with the hydrogen-bond network that had been proposed to facilitate proton release from Y_Z. The finding is consistent, however, with the previously reported absence of any electronic coupling between the tyrosine radical and any nitrogen atom (for a review, see Diner, 2001). The electron-density map allowed Fromme to propose a structural model for the tetramanganese cluster involved in water oxidation. In the most likely arrangement, three manganese atoms would be strongly coupled to one another and the fourth weakly coupled to the other three.

Another useful technique for studying the reaction centres is high-field electron paramagnetic resonance (HFEPR). This provides invaluable information about the distances between redox cofactors, their orientation and the interactions between a free radical and its protein environment under 'native' conditions. Using this strategy to study PSII, S. Un (Saclay, France) was able to measure the angular orientations of the different radicals that are transiently generated during PSII activity. This information complements the crystallographic structure, which, even at its current resolution, provides only the overall protein topology of the complex and the positions of the electron transfer cofactors. HFEPR can also be used in a classical spectroscopic approach to characterize the interactions between the redox cofactors and the nearby residues. These interactions, such as hydrogen bonds, have an important role in determining the redox properties of the electron-transfer components.

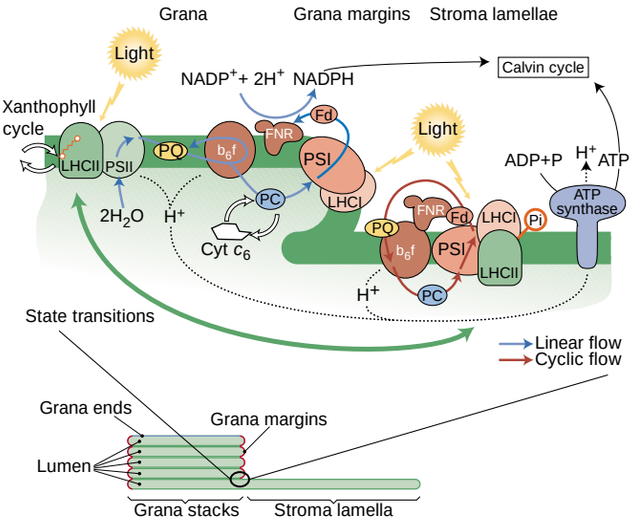

Fig. 3 | The thylakoid membranes and their domains, and the dynamics of the photosynthetic electron-flow machinery. In the thylakoid membranes (lower panel), photosynthetic activity results from the balance between light absorption and utilization. Several dynamic processes regulate the absorption of light: thermal dissipation in the photosystem II (PSII) outer antenna light-harvesting complex II (LHCII) is modulated by the xanthophyll cycle. Phosphorylation induces the reversible migration of this subcomplex from PSII to PSI (a state transition), which adjusts the relative absorption properties of the two photosystems and allows for the optimization of their relative activities. This dynamic regulation of photosynthesis also involves electron transport. Alternative electron carriers can be recruited depending on nutrient availability. The copper-containing plastocyanin (PC) enzyme can be replaced by cytochrome c_6 (Cyt c_6) under conditions of Cu^{2+} deficiency. In addition, supramolecular structures, granal stacks, the uneven distribution of complexes, and protein–protein interactions result in compartmentalization of the photosynthetic complexes and electron carriers. This is likely to modulate the efficiency of linear (blue) and cyclic (red) electron flow, and thus that of ATP synthesis, through the generation of a H^+ gradient. Fd, ferredoxin; FNR, Fd:$NADP^+$ reductase; PQ, plastoquinone. (Image drawn by Nicolas Roggli, University of Geneva, Switzerland.)

Supramolecular features of the photosynthetic apparatus

Structural and functional studies of the antenna rings that surround the reaction centers of photosynthetic bacteria (discussed above) have led to the concept of the supramolecular organization of the electron-transport chain.

In plants and algae, the peculiar arrangement of the thylakoid membranes might result in the compartmentalization of photosynthetic complexes. The thylakoids comprise stacks of vesicles (the grana) that are connected by unstacked regions (the stromal lamellae), with an uneven distribution of complexes between the two regions (Fig. 3). New insights into this structure and the mechanism of grana formation in native thylakoid membranes were presented by Z. Reich (Rehovot, Israel), who used scanning-force microscopy to obtain images of native, hydrated specimens at up to 3-nm lateral resolution and 0.3-nm vertical resolution. The images revealed detailed features of the thylakoid surfaces, including the distribution of individual proteins across the

stroma, grana margin, and grana-end membrane domains. Using immunogold labelling, Reich was able to identify two of the photosynthetic complexes (PSI and the ATP synthase) in the membranes, and to visualize their high density at the grana margins.

The consequences of compartmentalizing photosynthetic activity have been analysed by P. Joliot (Paris, France). He showed that cyclic electron flow around the PSI complex (Fig. 3) operates at a rate that is close to the maximum turnover of photosynthetic flow during the first seconds of illumination of dark-adapted leaves. This high efficiency implies that the cyclic and linear transfer processes (between the PSI and PSII complexes) do not compete with one another, and therefore that they are structurally isolated. According to Joliot's model, the cyclic pathway would operate within a supercomplex that is present in stromal lamellae and includes stoichiometric amounts of PSI, the cytochrome b_6f complex, plastocyanin and ferredoxin. Consistent with this possibility are results from the analysis of an engineered *Arabidopsis* line (generated in the laboratory of H.V. Scheller). In this line, the gene producing the PSI subunit PsaF, which is required to dock plastocyanin to PSI, is silenced by antisense RNA, and this results in an inhibition of cyclic electron flow.

Another example of limited diffusion in photosynthetic membranes that greatly influences the overall photosynthetic activity is provided by the state transitions that occur in *Chlamydomonas*, in which the fraction of LHCII that migrates between PSII and PSI is greater (up to 80%) than in other photosynthetic organisms (~15–20%). G. Finazzi (Paris, France) showed that state transitions in this alga result not only in changes in the absorption properties of the two photosystems, but also in a reversible switch between linear and cyclic electron flow. This is probably due to the significant protein rearrangement that occurs in thylakoid membranes in response to the movement of LHCII, and the consequent modifications in the diffusion properties of the hydrophobic electron carriers.

Metabolism

Photosynthesis drives not only CO_2 fixation, but also several other biochemical activities in the plastid, such as nitrogen assimilation and the biosynthesis of amino acids, fatty acids, starch and secondary metabolites. All of these processes are intimately related, as underlined by M. Stitt (Golm, Germany). He pointed out that the interplay between different metabolic pathways is not achieved solely through the regulation of the so-called 'rate-limiting' enzymes. Indeed, a 'global target analysis' of the main metabolic species ('metabolomics') has revealed several strategies that modulate metabolic responses. For example, interactions between the nitrogen and secondary metabolism pathways seem to occur at the level of specific metabolic precursors, such as glutamine, the levels of which correlate negatively with levels of the nitrate reductase transcript. A more general response is also induced by changes in sugar accumulation. These effects of the metabolites on gene expression are complementary to the effects of nitrate: they induce the genes for nitrate transporters and nitrate reductase, and stimulate the post-translational activation of nitrate reductase itself.

Exchange of metabolites between the plastid and the surrounding cytosol is mediated by a large number of transporters. U.-I. Flügge (Cologne, Germany) reviewed the nature and physiological properties of transporters that are located in the inner envelope membrane, and showed examples of the compensation ability of the different pathways that are implicated in solute transport across the chloroplast membranes. For example, the *Arabidopsis tpt-1* mutant is defective in the chloroplast triose phosphate/phosphate translocator (TPT). Nonetheless, the lack of triose phosphate for use in the synthesis of cytosolic sucrose is almost fully compensated for both by continuously accelerated starch turnover and by the export of neutral sugars from the stroma throughout the day. Crosses of *tpt-1* with mutants that are unable to mobilize starch (*sex1*) or to synthesize starch (*adg1-1*) revealed that growth and photosynthesis of the double mutants was severely impaired only when starch biosynthesis, but not its mobilization, was affected.

N. Rolland (Grenoble, France) pointed out that, in spite of their well-known physiological characterization, most of the proteins involved in ion and metabolite transport across the chloroplast envelope have not been identified. For this reason, he has developed a new proteomic approach that is specifically designed to identify the most hydrophobic polypeptides of the envelope. The use of organic solvents during the first steps of extraction allows an enrichment for highly lipophilic proteins, and more than 100 proteins have been identified, including most of the previously known envelope transporters and more than 50 novel candidates.

Concluding remarks

Photosynthesis can be studied from many different angles. In Les Diablerets, biophysicists and biochemists showed mountainous profiles with high peaks, and physiologists shared their admiration for the stress resistance of pine trees covered with snow. Participants had a chance to share their ideas and challenge one another about the different perspectives of the field. Given the success of this interdisciplinary meeting, maybe the next one will extend the landscape even further to include a view of the ocean, with studies of the ecological and global aspects of photosynthesis.

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