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MEETING REPORT

Signals, Sensing, and Plant Primary Metabolism

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The Third Symposium *Signals, Sensing and Plant Primary Metabolism*, organized by the DFG Sonderforschungsbereich 429 (''Molecular Physiology, Energetics, and Regulation of Primary Metabolism in Plants'') was held on the beautiful premises of the World Heritage Site, Park Sanssouci, Potsdam, Germany, from April 26th to 29th 2006. The program covered regulatory aspects of plant primary metabolism and fascinated attendees by integrating physiological, structural, and biophysical data. Numerous national and international speakers followed the invitation to the symposium and presented their most recent data.

METABOLISM: PATHWAYS AND REGULATION

The introductory session was dedicated to metabolism and its regulation. **Mark Stitt** (Golm) focused on diurnally regulated genes - as much as 30%–50% of the *Arabidopsis thaliana* genes change their expression daily. Expression profiling, enzyme activities, and metabolite profiling upon carbon depletion or sugar re-addition and during prolonged darkness were used for a detailed analysis of the response of *A. thaliana* to changes in carbon supply to address sugar involvement in light/dark cycles. Microarray data (Thimm and others 2004) were compared with proteomics and metabolomics. There was no clear connection between the three sets of data; in total, 21 diurnally expressed enzymes were analyzed at the RNA level, as well as on the activity level, and showed very few correlations. Nevertheless, sugar was shown to strongly influence diurnal changes. Comparison of diurnal changes in wild type and the starchless phosphoglucomutase (*pgm*) mutant indicated that sugars modify the expression of many clock-regulated genes. Most of the changes in *pgm* are triggered by low sugar levels during the night rather than high levels in the light (Bläsing and others 2005). Candidate genes involved in sugar-dependent signaling pathways were identified (many of them are involved in protein turnover: 15 proteins are involved in ubiquitin targeting). **Lee Sweetlove** (Oxford) highlighted post-translational networking of sequential enzymes of the same metabolic pathway by physical interaction, focusing on glycolytic enzymes that may form large protein complexes at the outer mitochondrial membrane. Using 2D blue native gels, he presented arguments for the phenomenon of substrate channeling of glycolytic enzymes in complexes called ''metabolons.'' **Alison Smith** (Norwich) summarized not-yet-textbook knowledge on starch breakdown pathways. Starch degradation in *Arabidopsis* leaves at night is significantly different from conventional knowledge: a glucan-water-dikinase (SEX1) cleaves starch—it

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seems to be an exo- rather than an endo-attack (as in case of α-amylase). Later, linear glucans derived from starch granules are hydrolyzed via β-amylase to maltose, which is exported from chloroplasts via a recently discovered maltose transporter (MEX1). In the cytosol, maltose is the substrate for a transglucosylation reaction, producing glucose and a glucosylated acceptor molecule. The described pathway may operate in organs that accumulate starch transiently. However, in starch-storage organs (cereal endosperm and legume seeds), the process differs from that in *Arabidopsis*.

Six further talks completed the session and the first day of the conference: **Frederik Börnke** (Erlangen) presented data on sucrose synthesis in tobacco leaves, focusing on two enzymes, sucrose phosphate synthase (SPS) and sucrose phosphate phosphatase (SPP). The latter enzyme is not rate-limiting, and RNAi plants did not show a major phenotype. In contrast, SPS is the key regulatory enzyme. At least three SPS genes were found in tobacco; all were analyzed by an RNAi approach and may have different functions. **Claudia Jonak** (Vienna) provided evidence for a role of a glycogen synthase kinase (MSK4) in salt stress tolerance. Overexpression of MSK4 in *A. thaliana* resulted in enhanced tolerance through accumulation of osmoprotectors like raffinose and galactinol. A new approach to analyze enzyme activities in *Arabidopsis* embryos by *in situ* histochemistry was presented by **Sébastien Baud** (York). Using a large-scale approach, it was demonstrated that glycolytic enzyme activities change during embryo development and in different embryo-lethal mutants. **Thomas Roitsch** (Würzburg) reported on the involvement of the cell wall invertase Nin88 from tobacco in pollen development and germination. Pollen of *Nin88*-antisense plants does not show tube growth, and *Nin88* gene expression is induced during pollen tube growth in wild-type plants. Competition uptake experiments showed that both sucrose and glucose are taken up by growing pollen tubes, confirming published data (Hackel and others 2006). It was shown that glucose is sufficient for pollen germination, but not for pollen tube growth. Additionally, it was concluded that a disaccharide signal is important for pollen tube elongation. **Stefan Binder** (Ulm) characterized the branched-chain aminotransferase gene family from *A. thaliana* (AtBCAT), its intracellular localization, and its involvement in amino acid metabolism. AtBCAT4 may be involved in methionine and glucosinolate biosynthesis, together with AtMAM1. **Andreas Meyer** (Heidelberg) presented new results on glutathione biosynthesis. Glutathione is normally synthesized in plastids through GSH1 and GSH2. However, GSH2 mutants indicate that the interim product, γ-glutamylcysteine, is rapidly transported out of the plastid to avoid feedback inhibition of GSH1. Hence, GSH2 may also work in the cytosol to form glutathione.

Transport

The transport session focused on organellar transporter proteins, which in the past few years have gained attention because of new insights into starch metabolism and breakdown during the night. **Ulf-Ingo Flügge** (Cologne) reported on three classes of phosphate transporters from the chloroplast inner envelope membrane (pPT genes). These antiport systems are specific for different intermediates, for example, triosephosphates (TPT), phosphoenolpyruvate (PPT) or pentose- (XPT), and hexose-phosphate (GPT). The transporters are crucial for the massive exchange of precursor molecules between cytosol and plastid stroma, allowing for communication between the compartments. Data emphasizing the impact of plastidic solute transporters for the path of carbon during night and day and for starch biosynthesis were presented: whereas the triose phosphate translocator (TPT) is important for the day path of newly fixed carbon, the night path of carbon allocation involves transporters different from the TPT. Starch breakdown results in the formation of maltose (exported via the maltose transporter MEX1) and maltotriose, which can be converted into glucose (exported via the putative glucose transporter pGlcT). Plastids of non-green tissues can import carbon in the form of glucose 6-phosphate by the GPT. The function of PPT transporters in plants is not fully understood. The proposed function of the PPT in C3 plants is import rather than export of PEP. PEP is required as a precursor for the plastid-localized shikimate pathway, from which aromatic amino acids and an array of secondary plant products derive. The *cue1* mutant with lowered CAB expression is defective in a PPT, and the mutant phenotype can be rescued by feeding aromatic amino acids or cytokinins as well as by ectopic overexpression of PPT. AtPPT1 might be involved in the generation of a signal molecule, which has the potential to trigger the correct mesophyll development. **Ekkehard Neuhaus** (Kaiserslautern) pointed to the function of the ATP/ADP transporter in chloroplasts, which, in contrast to ADP/ATP transporters from heterotrophic plastids, are not required for energization of the chloroplast stroma. The analysis of ntt1 and ntt2 mutants and double mutants showed high

accumulation of protoporphyrinogen IX and changes in Mg- and Fe-Chelatase activities. The role of the chloroplastic ATP/ADP transporter was shown to be important in the chlorophyll and heme biosynthetic pathway (Mg-Chelatase activity in contrast to Fe-Chelatase is ATP-dependent). **Uwe Nehls** (Tübingen) analyzed plant–ectomycorrhiza interaction depending on the availability of carbohydrates by manipulating the host: poplar plants overexpressing a monosaccharide transporter from *Vicia faba* showed improved shoot growth and photosynthetic capacity, whereas root development was unaltered. The plants showed a significantly lower degree of mycorrhization, arguing for competition of host and symbiont for monosaccharides. Ectomycorrhiza microarray analysis may help to identify candidate genes important for the plant–mycorrhiza symbiosis. **Ralf Bernd Klösgen** (Halle) focused on one out of four protein transport pathways operating in the thylakoid membrane: the ΔpH-dependent twin-argininine-translocation (Tat) pathway able to transport folded polypeptide chains. Transport by this pathway requires thylakoid targeting signal peptides carrying a twin pair of arginine residues upstream of the hydrophobic core domain. Tat translocase consists of three components TatA, TatB, and TatC. Whereas TatB and TatC are involved in substrate recognition, TatA might be the major pore-forming component. The mechanism of protein translocation via the Tat pathway was studied using a chimeric 16/23 precursor polypeptide consisting of the 16 kDa transit peptide fused to the mature 23 kDa part of the protein. Using antibodies and blue native PAGE, it was found that the chimeric 16/23 model substrate is complexed with TatB/C during thylakoid transport and that the assembly of all three subunits is required for protein translocation.

Sensors and Signaling

Sensors and signals were a central topic of the conference—even providing its name. Talks in this session covered nearly the whole range of plant signaling; major contributions focused on redox regulation, organellar signaling, and sugar sensing. The session was opened by **Bob Buchanan** (Berkeley), who presented an outlook on the broadened horizon of redox regulation. Focusing on the thioredoxin protein family in plants, he pointed out that today's knowledge, based especially on advances in proteomics approaches, indicates that plant thioredoxins regulate processes at virtually every stage of plant development. Recent research has not only revealed hundreds of thioredoxin-linked proteins but also uncovered new types of regulation and modes of communication. In addition to a general overview, Buchanan stressed the importance of redox changes during seed development, as well as in the wheat amyloplast system. Coming to technological issues such as the use of overexpressed thioredoxin to enhance digestibility of *Sorghum*, he finally emphasized the applicability as well as the importance of basic research on plant redox regulation. Following the comprehensive introduction, a number of speakers gave reports on specific examples of redox regulation. **Margarethe Baier** (Bielefeld) presented work on redox regulation of the nuclear 2CPA gene encoding a chloroplast 2-Cys peroxiredoxin (2CPA). A redox-sensitive domain of the 2CPA promoter had been characterized and was now used to identify a transcriptional activator that could provide a link between signals derived from chloroplasts, abiotic stress, and the metabolic status of the cell. **Thomas Pfannschmidt** (Jena) gave an introduction into redox-regulated signaling pathways of short-term and long-term responses involved in light acclimation. Pfannschmidt and coworkers had shown earlier that long-term responses (LTR) to light quality changes involve a photosystem stoichiometry adjustment by redox signals from photosynthetic electron transport. Studies with *Arabidopsis*, using macroarrays and photoreceptor mutants, showed a coupling of nuclear genes to chloroplast expression events and an independence of photosystem adjustments from photoreceptors. The presented work established chloroplast redox signals as a separate and novel class of plastid signals, thereby elegantly bridging the gap from redox to plastid signaling. **Dario Leister** (Munich) was deepening the chloroplast-to-nucleus signaling topic by introducing work on the impact of post-translational modifications and organellar translation rates. Characterization of *Arabidopsis* LHC II-kinase mutants *stn7* and *stn8* defective in state transition illustrated that both kinases act in parallel and may be directly responsible for phosphorylating LHC II and photosystem II core proteins, respectively. Furthermore, *stn7* mutants are not showing the LTR in light acclimation, implying that STN7 has a function in coordinating LTR and short-term responses to changes in light conditions. However, the nature of the signal and how it is transferred to the nucleus remains an open question that Leister and coworkers are trying to address at present. **Agepati Rhagavendra** (Hyderabad) summarized current ideas regarding interactions of the metabolic reactions in different organelles of the plant

cell, focusing on possible signaling functions of ascorbate and nitric oxide. Bringing the topic once more back to redox control, **Michael Hothorn** (Heidelberg) reported recent progress in understanding the regulation of plant glutathion biosynthesis. The crystal structure of substrate bound γ-glutamylcysteine synthetase revealed a two-component regulatory mechanism based on redox-sensitive disulfide bridges. An overview lecture given by **Filip Rolland** (Leuven) on sugar sensing emphasized the importance of another class of signals and corresponding sensors. Work on *Arabidopsis* sugar signaling mutants such as glucose insensitive (*gin*) and glucose oversensitive (*glo*) revealed extensive interactions between sugar and hormone signaling, and a central role for hexokinase as a conserved glucose sensor. Furthermore, recent findings suggest important and complex roles for Snf1-related kinases, extracellular sugar sensors, and trehalose metabolism in plant sugar signaling. Protein kinases also played a central role in the talk given by **Markus Teige** (Vienna), who reported on molecular mechanisms involved in adaptation to cold and salt stress. His group demonstrated that specific responses were mediated by MAP-kinases, as well as by calcium-dependent protein kinases (CPKs). Details on the localization and molecular targets for these enzymes were discussed. Finally, the last speaker in the signaling session, **Peter Hegemann** (Berlin) introduced sensory photoreceptors such as Channelrhodopsin-1 and 2 (ChR 1 and 2) from *Chlamydomonas*. ChR 1 and 2 are light-gated ion channels that are localized in the algal eyespot membrane. Upon illumination, the ChRs depolarize the eyespot membrane sensed by voltage-gated Ca^{2+}-channels, mediating a weak to strong Ca^{2+}-influx ultimately modulating flagellar beating. *Chlamydomonas* cells contain at least 7 different rhodopsins, a chryptochrome, a phototropin and probably a phytochrome-like receptor.

Supramolecular Complexes

The session on supramolecular organization of plant and cyanobacterial energy converting systems was started by **Jan Kern** (Berlin) with a report on the most recent developments in structure elucidation of cyanobacterial photosystem (PS) II, as recently reported by Loll and others (2005). The hitherto unprecedented resolution (3.0 Å) is a further step ''towards complete cofactor arrangement'' providing novel insight into functional aspects of the ''heart'' of oxygenic photosynthesis. Exact locations of 20 protein subunits and 77 cofactors per monomeric subunit were established. Assignment of 11 β-carotene molecules yields further insight into energy transfer and photoprotective mechanisms in the PS II reaction center and antenna system. The structural and functional importance of 14 integrally bound lipids was highlighted. Moreover, a lipophilic pathway for the diffusion of Q_B from its binding site to the electron transfer chain was proposed. **Hans-Peter Braun** (Hannover) reviewed recent advances in the elucidation of supercomplex formation in the mitochondrial respiratory chain (see also Dudkina and others 2006). Using blue native PAGE, they were able to characterize supercomplexes composed, for example, of complexes I and III. Furthermore, a 3D structure of complex I was proposed, which in plants—in contrast to animals—has an additional domain formed by carbonic anhydrases, which play a role in CO_2 metabolism. **Lutz Eichacker** (Munich) reported on the regulation of photosystem assembly. **Wolfgang Loeffelhardt** (Vienna) introduced eukaryotic ''carboxysomes'' to the audience—microcompartments involved in the carbon-concentrating mechanism in cyanelles of *Cyanophora paradoxa*. **Jean-David Rochaix** (Geneva) presented data on ''Assembly and dynamics of photosynthetic complexes in *Chlamydomonas* and *Arabidopsis*.'' Tab1/Tab2 proteins are RNA-binding proteins that appear to play a role in PSI assembly. The importance of the stt7 kinase for state 1-state 2-transitions, regulating excitation energy distribution between PSII and PSI was highlighted. **Wolfgang Hähnel** (Freiburg) described approaches to detect low abundance chloroplast proteins using 2D gels and Nano-LC hybrid mass spectrometry. The ensuing talk, by **Harald Paulsen** (Mainz), dealt with the elucidation of the sequential steps in the assembly of the major light-harvesting chlorophyll-*a/b* complex (LHC II).

Photosynthesis: Regulation and Mechanisms

One focal point of the meeting was photosynthesis and its regulation. Following the session on structure and assembly of the photosynthetic apparatus, functional and—in particular—regulatory aspects were covered in the next three sessions. **Thomas Renger** (Berlin) started introducing theoretical approaches to describe excitation energy transfer (EET) in photosynthetic light-harvesting complexes (LHCs). Two mechanistic cases were discussed: weak coupling between pigments (described by conventional Förster theory) and strong (excitonic) coupling between pigments. These approaches were used to describe EET in the main light-harvesting complex, LHC II on the basis of the recent highly resolved structural models and previous site-direc-

ted mutagenesis studies. The outline given in Renger's talk was detailed in several related poster contributions. **Peter Nixon** (London) presented new data on quality control and degradation of damaged D1 reaction centers in *Synechocystis* and *Arabidopsis*. In this regard, the FtsH protein appears to play an important role, because mutants in *Synechocystis* show disturbed D1 turnover and are, consequently, very sensitive to high and even moderate light intensities. The talk presented by **Alfred R. Holzwarth** (Mülheim) may help to topple a long-standing paradigm: using femtosecond time-resolved spectroscopy and highly sophisticated data analysis to investigate kinetics and mechanisms of EET and electron transfer in PSII from *Thermosynechococcus*. Holzwarth challenged the conventional view that the so-called special pair of chlorophyll *a* is the primary donor in PSII (similar to in the reaction center of purple bacteria). He provided further evidence that the so-called accessory chlorophyll *a* is the primary electron donor and pheophytin is the primary electron acceptor in PSII. In PSI, the mechanism of primary charge separation appears to be different (Holzwarth and others 2006). **Roberta Croce** (Trento) discussed the functions of the (at least) four different light-harvesting complexes of plant PSI. From experiments with mutant reconstituted LHCs it is concluded that the characteristic 735 nm low-temperature fluorescence maximum of PSI is due to a special pigment arrangement. **Peter Jahns** (Düsseldorf) talked about functions and regulation of the xanthophyll cycle in plant light-stress responses, highlighting in particular the role of the xanthophyll-binding LHC proteins. Zeaxanthin appears to have two major functions, in dissipation of excess singlet and triplet excitation energy, and as an antioxidant. Three different pools of violaxanthin were established, in accordance with previous studies (Härtel and others 1996). Carotenoid biosynthesis mutants showing different tolerance to high and low light were compared. **Graham Fleming** (Berkeley) closed the last session that day with two talks, the first dealing also with the highly controversially discussed field of regulation of photosynthetic light harvesting. The presentation focused on novel aspects of the mechanism of excess excitation energy quenching in plants (involving the xanthophyll cycle and the Psbs protein). It was proposed that chlorophyll to zeaxanthin charge transfer and subsequent carotenoid radical formation is the mechanistic basis of excess energy dissipation (Holt and others 2005).

Fleming's second presentation—an address to all scientists concerned with aspects of plant metabolism and bioenergetics—drastically depicted scenarios of near-future global climate changes (in particular, the issue of ''hot-house gas'' emissions from burning fossil fuels and consequent global warming). The audience was urgently called on to devise sustainable sources of energy to prevent—or even revert if still possible?—the imminent catastrophic events. Although the talk did not prevent the conferees from enjoying the splendid dinner that followed at the historic windmill in Sanssouci Park, it certainly inspired the ensuing discussions.

Regulatory aspects of photosynthesis were also the focus of the early-morning session on Saturday. **Ayumi Tanaka** (Sapporo) started the session with a report on the identification of a protease involved in the regulation of the stability of the chlorophyll *b* biosynthetic enzyme, CAO (see also Hirashima and others 2006). The enzyme was shown to be important for the adaptation of antenna size to ambient light conditions. **Herbert van Amerongen** (Wageningen) further discussed EET (and its regulation) in PSII. In his talk he purported that LHC II can switch between a light-harvesting and a quenched state via a conformational change. **Ken'ichi Ogawa** (Okayama) reported that plant growth and pathogen-related responses (both of which are mediated by photosynthesis) are regulated by glutathionylation of a single protein.

Plant Metabolism

The last session closed the circle by coming back to plant metabolism and its regulation. **Bernd Müller-Röber** (Golm) pointed out the transcriptional control of leaf physiology and development. Transcription factor (TF) profiling was performed by co-response analysis with leaf metabolic pathway enzymes and quantitative real-time polymerase chain reaction (PCR) to identify candidates that are upregulated or downregulated during leaf sink-source transition. Further analysis focused on the group of the Dof-type TFs, belonging to the zinc finger TF family, by overexpression or RNAi-repression of single Dof genes. **Ralph Bock** (Golm) introduced interesting new tools for plant biotechnology. His group uses the technique of plastid transformation offering many advantages over conventional approaches to engineer metabolic pathways in crop plants: high expression levels of foreign proteins (>20% of the total cellular protein), absence of epigenetic and position effects, and efficient translation of polycistronic messengers (Bock 2001; Ruf and others 2001). An additional advantage is the maternal inheritance of the plas-

tid genome, which reduces the risk of uncontrolled propagation of the transgene. The chloroplast transformation system has been improved for tomato plants, allowing the expression of foreign genes not only in leaves but also in fruits (Ruf and others 2001). Chromoplasts in the transplastomic plants express the transgene to approximately 50% of the expression in leaf chloroplasts. **Thomas Schmülling** (Berlin) talked about the influence of cytokinins on sink capacity of roots and shoots. The cytokinin deficiency syndrome (CDS) as induced by overexpression of the cytokinin-catabolizing enzyme cytokinin oxidase (CKX) in transgenic plants causes pleiotropic effects: reduced shoot growth, enhanced root development by triggering cell differentiation in meristems of roots and shoots in opposite ways. Cytokinin deficiency syndrome seems to be partially due to reduction of trehalose-6-phosphate. Further analysis involved the search for suppressor mutants of the CDS as well as tissue-specific downregulation of the cytokinin content in transgenic plants. **Teresa Fitzpatrick** (Zürich) presented new data on the plant vitamin B_6 (pyridoxine) biosynthetic pathway. Comparing the plant pathway with that from gram-negative bacteria (*Escherichia coli*), it was concluded that what is true for *E. coli* is not necessarily true for the elephant (an allusion to Jacques Monod). The vitamin B_6 biosynthesis pathway is exclusively found in microorganisms and plants and has been intensively studied in the gram-negative bacterium *E. coli*. However, most other organisms use a different pathway for vitamin B_6 biosynthesis involving the two genes, PDX1 and PDX2, that do not have homologs in *E. coli*. The two proteins form a complex that functions as a glutamine amidotransferase with PDX2 as the glutaminase domain and PDX1 as the acceptor and pyridoxalphosphate synthesis domain (Raschle and others 2005).

Arabidopsis thaliana has three homologs of PDX1 showing different tissue-specificities and a single homolog of PDX2. **Lothar Willmitzer** (Golm) closed the session and meeting by proposing novel approaches for plant systems biology. His final remarks highlighted metabolomics, transcriptomics, and proteomics—approaches that should precede the detailed analysis of single genes. The power of genome-wide metabolite profiling for identification of quantitative trait loci (QTLs) was demonstrated by tomato introgression line (IL) profiling. For the identification of new genes responsible for metabolite composition, profiling of the metabolite and transcript level under altered environmental conditions was suggested, followed by analysis of correlations and networks by co-response studies to identify candidate genes or small signaling molecules.

Posters

The talks were supplemented by about 80 excellent posters. One very exciting presentation should be highlighted here: for the first time, a fluorescent amino acid sensor was shown to be functional in plants cells. Martin Bogner from the group of **Uwe Ludewig** (Tübingen) presented unpublished data showing that use of the FRET-based technique of arginine (and glutamine) binding proteins made it possible to measure internal arginine concentrations in plant protoplasts as well as in stably transformed *Arabidopsis* plants. The sensor is based on the bacterial GlnH protein from *E. coli*, which binds glutamine with high affinity. Two different green fluorescent proteins were attached to GlnH, and FRET was measured in *E. coli*, yeast, and plants. Emission changed upon arginine supply. Thus this fluorescent amino acid sensor seems to be a versatile tool for reporting amino acid dynamics in living plant cells.

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