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HISTORY AND BIOGRAPHY

In memory of Achim Trebst (1929–2017): a pioneer of photosynthesis research

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Abstract
The life and work of Achim Trebst (1929–2017) was dedicated to photosynthesis, involving a wide span of seminal contributions which cumulated in more than five decades of active research: Major topics include the separation of light and dark phases in photosynthesis, the elucidation of photosynthesis by the use of inhibitors, the identification of the three-dimensional structure of photosystem II and its degradation, and an explanation of singlet oxygen formation. For this tribute, which has been initiated by Govindjee, twenty-two personal tributes by former coworkers, scientific friends, and his family have been compiled and combined with an introduction tracing the different stages of Achim Trebst's scientific life.

Keywords Photosynthetic electron transport · Light and dark phases · Inhibitors · Photosystem II · Singlet oxygen

Introduction

On the occasion of his 80th birthday in 2009, the extraordinary achievements of Achim Trebst in the field of photosynthesis research have been honored by three scientific reviews compiled by Volker ter Meulen and Rolf Thauer (Ter Meulen and Thauer 2009), Heinrich Strotmann (Strotmann 2009), and Walter Oettmeier (Oettmeier 2009), supplemented by a personal tribute by Govindjee (Govindjee 2009), all of which were published in this journal. Only 1 year earlier, in 2008, the last scientific contribution of Achim Trebst had been published (Krieger-Liszkay et al. 2008). Regrettably, Achim Trebst passed away on September 4th, 2017. With the present appreciation, it cannot be the aim to recapitulate the reviews of 2009, but instead twenty-one different tributes, written by former coworkers or scientific friends, accompanied by a family account from his second son Simon Trebst, will now honor the outstanding personality and accomplishments of Achim Trebst. The present text is an appreciation of Achim Trebst's scientific career that mainly points out facets that, so far, have not been highlighted.

Achim Trebst was born in Zeitz, a small city in the federal state Saxony-Anhalt in the Eastern part of Germany, on June 9th, 1929. Early in his childhood, the family moved to Hanau, a city south of Frankfurt, where his father ran a doctor's office. After graduating from the gymnasium with a German *Abitur*, he started as an apprentice in a pharmacy. Two years later, he began to study chemistry at the University of Heidelberg. In the laboratory of Friedrich Weygand, he took up graduate studies and completed his doctoral thesis in 1955. His first publication (Weygand et al. 1954) was already indicative for his research in subsequent years in which he studied the biosynthesis of components of DNA through the use of bacteria and radioactive isotopes. Using the same tools, bacterial cells, and radiolabeled biosynthetic precursors, eight papers followed with topics including the biosynthesis of coenzyme F (N^{10} formyltetrahydrofolic acid) and the incorporation of compounds such as 5-bromouracil or sulfanilamide into the bacterial metabolism. All of Achim's publications at that time were written in German, and almost all were published in the journal *Zeitschrift für Naturforschung*. This journal remained his favorite over his life, despite its relatively low impact factor, true to his

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philosophy that the scientific quality of his papers was sufficiently outstanding to be recognized regardless of a journal's reputation.

Achim followed his mentor Weygand who got positions first in Tübingen (1953) and then in Berlin (1955). In the German capital, he came into contact with the Nobel prize winner Otto Warburg and started to run experiments under his guidance. However, Warburg preferred to work with technical assistants, typically trained in physics, rather than working with postdoctoral researchers. Therefore, from 1956 until 1958 Achim joined the group of Daniel Arnon in Berkeley as postdoctoral fellow (Fig. 1). Berkeley was then the center of photosynthesis research. Melvin Calvin had elucidated the CO_2-fixation cycle and the enzymes involved and was honored with a Nobel Prize in 1961. Daniel Arnon (Fig. 2) had worked on photosynthetic electron transport, had discovered cyclic photophosphorylation and the involvement of ferredoxin in plastidic photosynthesis—but was not awarded a Nobel. Some kind of jealousy always existed between these two outstanding groups in Berkeley, which often prevented coworkers from both sides to come into close contact. Still, Achim Trebst met an impressive group of excellent scientists in Arnon's laboratory many of whom became professors and remained Achim's friends until the end. From the early Arnon time this includes F.R. (Bob) Whatley (later Oxford), Manuel Losada (Sevilla), and Bob Buchanan (Berkeley), and from the later period David O. Hall (London) and Reinhard Bachofen (Zürich).

Achim Trebst's postdoctoral research culminated in the Trebst, Tsujumoto, Arnon paper published in Nature in 1958 (Trebst et al. 1958), in which photosynthetic electron transport was shown to generate assimilatory power, namely, NADPH and ATP, which are required for the subsequent reduction of CO_2 (Fig. 3). Seven further publications on the subject followed during his period in Berkeley, with an extension of the findings to bacterial CO_2-fixation. Achim always considered himself fortunate to have spent his postdoctoral time in Berkeley during a period of exciting discoveries, which are valid until today and have become common textbook knowledge.

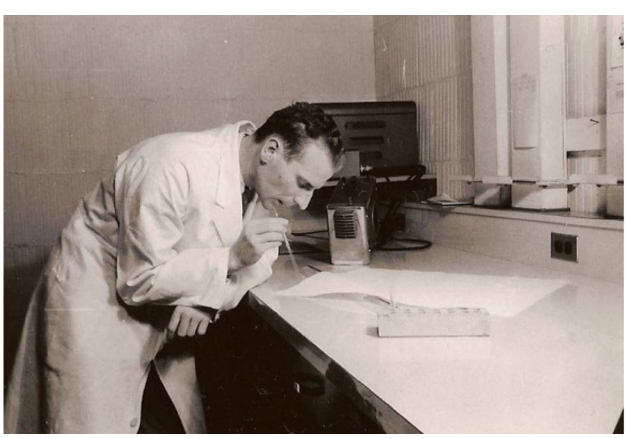

Fig. 1 Trebst at work in Daniel Arnon's lab at UC Berkeley (1956)

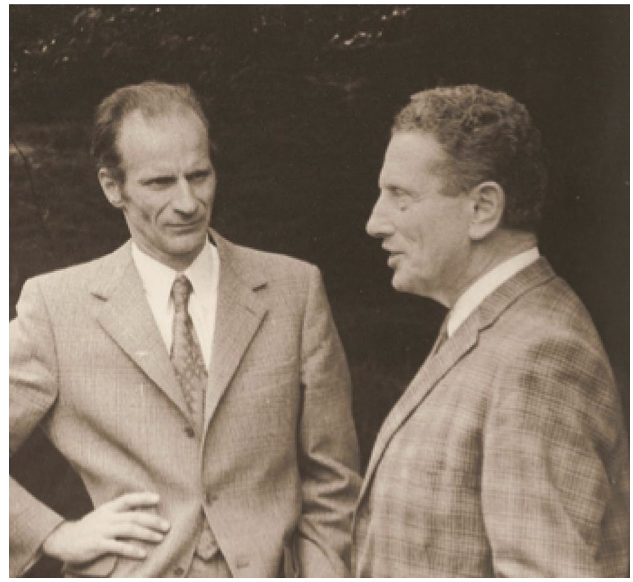

Fig. 2 Trebst and Arnon at Schloss Hammerstein (1972)

Achim Trebst returned to the laboratory of Weygand who had moved to Munich in the meantime. There Achim obtained his *Habilitation* (which in the German system has traditionally been the essential advanced degree before a young researcher can establish an independent laboratory and guide students autonomously). His first doctoral students Eck, Dorrer, and Fiedler performed studies on the roles of quinones in photosynthetic electron transport, the use of inhibitors to specifically block it, and the specific radioactive

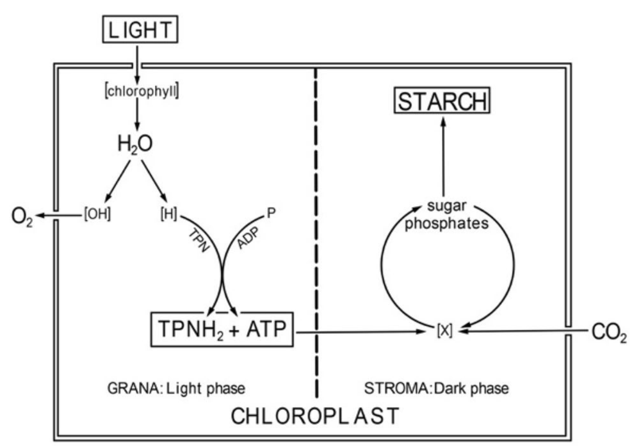

Fig. 3 Scheme for photosynthesis by isolated chloroplasts, Reproduced from Trebst et al. (1958). TPN is the former term of $NADP^+$

Fig. 4 1962 Conference on Photosynthesis in Paris. Arnon, Trebst, Vennesland, and Warburg

labeling of hexoses formed in photosynthesis (Fiedler et al. 1967) (Fig. 4).

In 1963, Achim Trebst accepted an associate professorship in Göttingen with the support of the then highly influential Professor André Pirson. Pirson, who was widely known for his discovery of the involvement of manganese in photosynthesis (Pirson 1937), had the capacity—as full professor in Göttingen—to attract an outstanding generation of younger researchers and colleagues that later became internationally highly recognized scientists. Both remained close friends until the end of Pirson's life in 2004. In Göttingen, Achim became quickly known to be very demanding to students in the laboratory courses, with the consequence that only the best students dared to start a thesis under his guidance: Carl Fedtke, Friedhelm Geike, Ahlert Schmidt, Herbert Böhme, Günter Regitz, Hermann Bothe, and Erich Elstner (who had joined him already in Munich). Another characteristic trait of Achim Trebst was that he was able to hire extremely capable technicians that were able to expertly conduct experiments even based on novel setups conceived during early morning discussions: Elfriede Pistorius in Göttingen and later, in Bochum, Susanne Reimer followed by Brigitte Depka.

Already in Göttingen, Achim Trebst started his long reaching and fruitful cooperation with the chemists Büchel and Draber from the Bayer company in Leverkusen. This work resulted in the discovery of new inhibitors of photosynthetic electron transport such as alkyl benzimidazole, carbamates, triazinones, and of artificial electron donors to photosystem I or II such as p-phenylenediamine. This approach culminated in the description of dibromothymoquinone (DBMIB) as a specific inhibitor at the acceptor (plastoquinone) side of photosystem II (Trebst et al. 1970; Böhme et al. 1971). Up to this day, DBMIB is used as specific tool to block photosynthetic electron transport in almost every photosynthesis laboratory around the globe. The work on inhibitors and artificial electron donors and acceptors has been summarized in detail by Oettmeier (2009, see also his present tribute).

In Göttingen, Achim met Bärbel (Barbara) Nührenberg, a Ph.D. student and later assistant in Pirson's laboratory. They married and raised four children, every one of whom pursued academic careers on their own.

In 1967, Achim Trebst accepted an offer as chair in plant biochemistry at the newly founded Ruhr-University of Bochum. The university subsequently became a center of biological research in Germany with chairs headed by Esser (general botany), Zenk (plant physiology), Hamann (plant taxonomy), and Schwartzkopff (general zoology) besides Achim Trebst. All of them became nationally highly recognized scientists during the course of their work in Bochum.

Although it took time to set up the new laboratories in Bochum, Achim Trebst managed, admirably, to resume his experimental work almost immediately after his leave from Göttingen. It was recognized at that time that electron carriers of the photosynthetic light reactions cannot only be arranged by their redox potential (resulting in the classical Z-scheme). More importantly, electron transport proteins are located either outside, inside, or on both sides of the thylakoid membranes which is the prerequisite for the vectorial electron transport and the generation of the H^+-gradient across the thylakoid membranes. Achim Trebst, together with his brilliant assistant and partner Günter Hauska, made key contributions to dissect the topology of the carriers along the thylakoids, particularly by using specific inhibitors identified by himself (Fig. 5). Antibodies, developed by Richard Berzborn in the laboratory, significantly contributed to elucidate the sidedness of the vectorial electron transport, particularly in the case of plastocyanin and NADPH:ferredoxin oxidoreductase. Achim summarized all these exciting findings, in the context of the current literature, in his highly cited Ann Rev Plant Physiol article (Trebst 1974), which served as the basis for future investigations by many researchers (see also Hauska et al. 1974; Trebst 2007).

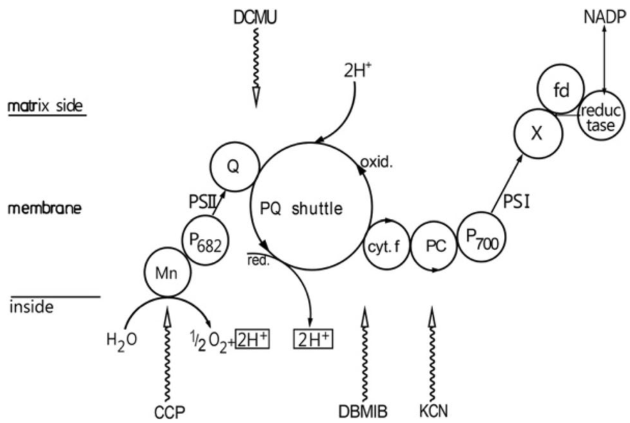

Fig. 5 Photosynthetic electron flow from water to NADP in a zig-zag across the membrane. Reproduced with permission from Trebst (1974)

Since the laboratory grew and grew, new research directions had to be taken up for the thesis work of the newly arriving coworkers (Fig. 6). This included the assimilatory sulfate reduction, which is also dependent on reduced ferredoxin and employs protein-related photosynthetic electron transport components, studied in detail by Schmidt, Schwenn, and Hennies. The activation of ribulose 1-5-bisphosphate carboxylase/oxygenase was characterized with much success by Wildner, while nitrogen fixation was the subject of Bothe, Godde studied chlororespiratory NADH oxidation by the microalga *Chlamydomonas reinhardtii* (Godde and Trebst 1980). Also, Achim Trebst was very early interested in the sustainable supply of energy and chemicals from renewable resources: Wolfgang Haehnel constructed galvanic cells for solar energy conversion using natural components in combination with artificial electron mediators, while Achim used engineered components of the photosynthetic electron transport chain to produce bio-hydrogen (Hoffmann et al. 1977). Later on, Happe characterized the hydrogen metabolism in green algae and isolated a novel type of hydrogenases with high potential for biotechnological applications. Johanningmeier developed the technique of transformation by a particle gun with emphasis on the generation of plastoquinone mutants.

Achim also preserved his love for microorganisms—founded in his early time in Weygand's laboratory—throughout life. He hired young promising group leaders for his institute in Bochum. The assistant professor Böger who worked with algae and cyanobacteria later moved as full professor to Konstanz. R. K. Thauer (Fig. 7) spent 3 years in Bochum as an associate professor and subsequently became director of the Max Planck Institute in Marburg (see tribute by Ter Meulen and Thauer 2009). He was succeeded by Altendorf, later full professor in Osnabrück.

Fig. 6 Achim Trebst holding the program for Botanikertagung in Marburg, Germany, September, 10–16, 1978. Back row (left to right): Ahlert Schmidt, Jens-Dirk Schwenn, Walter Oettmeier, Günther Wildner, Günter Eisbrenner, unidentified, and Peter Böger. Front row (left to right): unidentified, Richard Berzborn, Erich Elstner, Achim Trebst, Wolfgang Haehnel, and Herbert Böhme. Reproduced with permission from Oettmeier (2009)

Fig. 7 On the occasion of his 65th birthday (retirement), with Rolf Thauer

Since the reputation of the laboratory consistently grew, scientists from all over the world visited on an almost daily basis. In turn, Achim Trebst traveled a lot to countries all around the world giving talks at congresses and visiting laboratories. Many friendships and collaborations developed, of which only a few can be listed here. Achim often traveled to Sweden to visit H. and M. Baltscheffsky (former students of Chance) in Stockholm and Andersson, then in Linköping. He also developed a special love for Israel during many visits, held the position of a visiting professor at the Weizmann Institute of Science and became friends with excellent Israeli biochemists including Avron, Ohad, Malkin, Boussiba, Edelman, Hirschberg, and others. He also returned to Berkeley on a regular basis, even after Arnon had retired and Buchanan had assumed the position in Hilgard Hall. The cooperation with Sane, Mumbai/Lucknow, who often visited Bochum, and his friendship with Golbeck are particularly worth mentioning.

Achim Trebst's frequent visits at Cramer's laboratory in Purdue/West Lafayette—starting with a nine-month sabbatical in 1969—were of paramount importance. Both, together with the student Widger and in collaboration with Herrmann from Munich, compared the hydrophobicity of the polypeptide sequences of the photosynthetic cytochrome b_6f and the respiratory bc_1 complexes and noted their close relatedness and apparent joint evolution (Widger et al. 1984). This finding was subsequently extended to the situation in bacteria. By analyzing the primary amino acid sequences of the cytochrome *bc* complexes, Achim Trebst designed a model for their three-dimensional structure including the location of the heme groups (Fig. 8). Amazingly, these predictions proved to be essentially correct when the crystal structures of the complexes later became available.

Later work of Achim Trebst focused on the D1 protein of photosystem II and its herbicide-binding pocket(s) with remarkable success. Even after his retirement in 1994 and after Rögner had assumed the position of head of department in Bochum, he continued to work on the subject on a daily basis, together with his technician Depka and supported by the German funding agency DFG until his 80th birthday. He published on the modes of activity of the D1 and D2 proteins and their turnovers (Depka and Trebst 1997), the roles of singlet oxygen generated in photosystem II and of its scavengers such as tocopherol and carotene (Trebst et al. 2002). His work ended with the joint publication with Krieger-Liszkay and her team from Saclay on the glutathione peroxidase gene, which is specifically upregulated by singlet oxygen generated in photosystem II (Krieger-Liszkay et al. 2008).

Epilogue

Achim Trebst had a very sharp mind, capable to immediately analyze facts presented by his students or in talks at scientific congresses, while criticizing always in a helpful and constructive manner. He served as reviewer on numerous occasions on

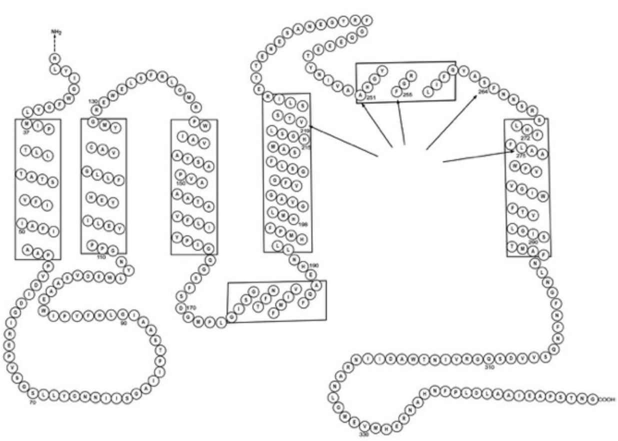

Fig. 8 The folding of the amino acid sequence of the D-1 polypeptide subunit of photosystem II. Reproduced with permission from Trebst (1987)

Fig. 9 Trebst during a lecture hosted by William A. Cramer at Purdue University, West Lafayette, IN, USA on the occasion of his honorary degree (2001)

the request of funding agencies or journals who appreciated that he was always critically but positively minded. He was an esteemed lecturer at numerous national and international congresses. For his outstanding achievements in the natural sciences, he received multiple extraordinary and well-deserved honors and awards. He obtained honorary doctorates from the universities of Stockholm (1990) and Purdue (1991), (Fig. 9). Exceptionally for Germany, Achim Trebst was also bestowed with an honorary doctorate by the University of Düsseldorf, not only because of his excellent scientific contributions but also for his significant help in the conception and organization of the newly founded Department of Biology in Düsseldorf (Strotmann 2009). He was elected as member of the National Academy of Science Leopoldina in Halle (1974) and of the North Rhine-Westphalia Academy of Sciences, Humanities and the Arts in Düsseldorf (1983)—honors which are reserved for only a very few scientists in Germany with exceptional achievements. Altogether, 50 students received their Ph.D. degree under his guidance. Furthermore, he promoted 14 young researchers for their Habilitation, and almost all of them later achieved professorships at German universities. Also, he published some 190 original scientific contributions. On September 4, 2017, with Achims Trebst's passing, the scientific community lost one of their most prominent and brilliant members.

Remembrances

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My first encounter with Achim Trebst was in 1958 as postdoctoral fellows at the Department of the late Professor Daniel I. Arnon, University of California, Berkeley. I learned much from him and we worked together for over 3 years in *photosynthesis by isolated chloroplasts*, especially in dependence of carbon dioxide assimilation on the photochemical generated "assimilatory power," comprising two components: $TPNH_2$ and ATP formed by the non-cyclic and cyclic photophosphorylation reactions (Losada et al. 1960).

Arnon was very quiet, careful, and meticulous in the planning and discussion of the experiments and in the final redaction of the papers. By contrast, Achim was very nervous and impatient and often literally jumped from his chair when Arnon repeated once and again for the umpteen time the same sentence or conclusion. This was especially the case when we discussed for hours, since Arnon was certainly very clear-minded but somewhat stubborn, and once he forced the editors of *The Journal of Biological Chemistry*

Fig. 10 Trebst and Losada in Yosemite National Park (1958)

to accept the abbreviation $TPNH_2$ instead of TPNH for the reduced form of triphosphopyridine nucleotide adducing stoichiometric reasons (see *JBC* 235, 832, 1960). The question was, and is even today, of great and far-reaching relevance, since it is the hydride ion (H^-), rather than the hydrogen molecule (H_2), the chemical species involved in the reduction of the nucleotide by water (H_2O).

Achim possessed a beautiful car and, since we were both bachelors, he took me with him to many picnics and excursions (Fig. 10). He even taught me how to drive, for I had never driven before nor owned an automobile. Our last experience was our trip to a meeting at Montreal, Canada. We worked then on carbon assimilation by photosynthetic bacteria and were very proud because we had identified in the radioautograph of a chromatogram a new spot, which was identified as citramalate, resulting from the condensation of acetyl CoA and pyruvate. Since it was the little brother of Ochoa's famous condensing enzyme, citrate synthase, we passed to see him on our return trip through New York. It was months before Ochoa had received his Nobel Price. He discussed with us very amiably and eagerly our "discovery." The corresponding paper was published in *Nature*, 1960. When we came back to Europe, we both visited Kandler and Lynen, and Achim invited me to give lectures at Göttingen and Bochum. He returned the visit coming to Seville.

On the return to our respective countries, we both made even more important discoveries and married enchanting wives and model mothers, Bärbel and Antonia.

He will be greatly missed by his friends and all the scientific community.

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Morning discussions stand out in the memories of postdocs who worked on photosynthesis with Daniel Arnon in Berkeley during the 1960s and 70s. Arnon was known for his strong personality that he exerted in running the laboratory. This resulted in a regimented atmosphere more typical of laboratories in Europe than the United States. The crux of Arnon's approach stemmed from his experience in his visit to Otto Warburg's laboratory in Berlin-Dahlem in 1956.

Thus, starting daily promptly at 8:30, Arnon would don a freshly starched white laboratory coat and begin his rounds. He would sit down with postdocs at their desks and discuss details of experiments to be carried out that day. Often Harry Tsujimoto, a mainstay of the laboratory joined the discussions. Later in life, the postdocs realized that these discussions were valuable and added to their training. However, at the time the discussions seemed lengthy, even tiring for impatient young scientists who wanted to get on with the work. Arnon's postdocs typically worked in pairs on projects he had assigned—the projects need not be in an area of their interest or expertise. In the present case, Achim Trebst from Germany teamed up with Manuel Losada, a Spaniard, to do important experiments that helped lay the foundation for our understanding of chloroplasts (Losada et al. 1960)—information now a part of contemporary textbooks.

There is a smorgasbord of stories describing Arnon's philosophy and approach to science brought out in these sessions. He usually started by taking a yellow manila pad and a mechanical pencil fitted with fine lead that he carried in his laboratory coat pocket. In a typical opening sentence, Arnon would state in a resonant voice, "Let's start with what we know." Referring to Priestley, Ingenhousz, or other luminaries, he would proceed to write the fundamental equation for photosynthesis, describing how the experiment of the day fits into this general picture. At this point, discussions took place between Arnon and the postdocs as there was usually disagreement on critical points. The best strategy for enabling a postdoc to follow his own ideas was to propose a solution opposing that of Arnon. This was eventually taken up and defended by Arnon with strong arguments for the postdoc's original concept.

The discussions were uniformly active and sometimes heated. The tolerance for these verbal exchanges varied among postdocs. Manuel Losada endured and even enjoyed the sessions, whereas Trebst, who was more reserved, felt awkward and would often slip away unnoticed in the heat of the discussion, only to emerge after the tone moderated. In a memorable session, Losada said, "Dr. Arnon you are stubborn, but I am more stubborn." With this the discussion ended for the morning.

I found this contrast between the former postdocs of interest. Both Trebst and Losada took advantage of their training and went on to distinguished careers that were fundamental in establishing the field of chloroplast biochemistry.

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In 1963 I knocked on Achim Trebst's door in Munich asking for an experimental diploma work. I left with the task of finding plants that would allow one to isolate intact chloroplasts harvestable even in winter and found primroses. Even as newcomer I was invited to attend the Nobel lectures at Lindau, where Otto Warburg´s talks were almost as important as the lunch we had on our way to Lindau. Shortly later, Trebst was invited as Professor in Göttingen and he offered me a position as a Ph.D. student to work on "The role of copper in photosynthetic electron transport." We established the electron transport (ET) around PS I by isolating PSI particles and the copper protein plastocyanin (Elstner et al. 1968).

During a new course in Biochemical Genetics I was in the "Boss's group": Achim Trebst designed the experiments, Elfi (Pistorius) carried them out with brilliance and I cared about sandwiches. Next Friday seminar my report on our results was poor and Achim Trebst was quick to inform me that I had to retry. He always acted as a wise teacher and like a father to me, whom I urgently needed. The "industrialized" production of plastocyanin was replaced by cytochrome *c* from Euglena cultured semi-automatically. Achim Trebst liked this "industrial" approach, which imploded one late evening. In summer the "Boss" initiated soccer games as geologists in limestone quarries with meat, beer, and hammers. In such events, we often had guests where I also met my wife Helga. In soccer, nobody could out-trick Hermann Bothe and the best-grilled meat was done by Herbert Böhme who also had the longest discussions on ATP-stoichiometry with Achim Trebst who loved topics that were not fully understood. The promotion of four candidates was the highlight of 1967, one of them being Bärbel Nührenberg, a student of Professor A. Pirson and his later wife. In 1968/69 Achim Trebst was offered a new institute at the Ruhr-University and I went to the laboratory of Robert Suhadolnik at the Albert Einstein Medical Center in Philadelphia to study nucleoside-biosyntheses with isotope techniques since Achim Trebst wanted me to gain the position of an "Akademischer Rat" in a manner of the unforgotten Adolf Kuhl of Göttingen. One of Achim Trebst's attributes was to instantly recognize specific virtues which then he stimulated with plenty of appreciation.

In 1972, back to Bochum, oxygen activation, ethylene biology, teaching, and habilitation governed daily life including the care of celebrations. In 1975, Rudolf Thauer, Günter Hauska, Hermann Bothe, and I left. My journey to Munich and Freising, Biochemical Phytopathology and Oxygen Biochemistry was always eagerly observed by Achim Trebst. Even far away, he was and will be always close to me.

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During the winter-term in 1964–1965, I joined a course at the Botanical Institute of the University of Göttingen. Prof. Trebst supervised us on measurements in photosynthesis the last month. At the end of that lab-course Prof. Trebst asked me whether I would like to join his group. He searched for a Ph.D. student being interested in investigating sulfate reduction for cysteine formation by chloroplasts. Nobody in his laboratory had worked on that subject until then. I was surprised and also pleased about that offer which I accepted from the summer term 1965 on. The broad and tentative title was "assimilatory sulfate reduction in plants." After a literature research for three weeks on recent developments in sulfur metabolism, Prof. Trebst and I agreed to work on ATP sulfurylase. I had to set up all experimental details and learn how to handle and purify enzymes. The first exciting finding was that extracts of isolated chloroplasts had a highly active ATP sulfurylase. Therefore, experiments were planned to label isolated chloroplasts with radioactive sulfate to follow any potential formation of cysteine with positive outcome. Thus assimilatory sulfate reduction of plants was shown to occur in chloroplasts (Schmidt and Trebst 1969). Subsequently, I centered my efforts on finding intermediates of sulfate reduction in chloroplasts. All these findings around this topic lead to the dissertation entitled "Investigations on sulphate reduction by isolated chloroplasts." My thesis was accepted without bigger changes by Prof. Trebst. In January 1969, I passed the final thesis examination under the auspices of the internationally highly recognized scientists Prof. Trebst (plant biochemistry), Prof. Pirson (botany), and Prof. Schlegel (microbiology). At that time, Prof. Trebst had accepted a position as a full professor in Bochum, and I joined him on an assistantship in April 1969 to set up a laboratory for sulfur metabolism. Two students recruited in Göttingen also came to the new Bochum laboratory to work on sulfite reductase (Hennies) and on plant sulfate assimilation (Schwenn). My studies focussed on the role of sulfonucleotides in assimilatory sulfate reduction. Prof. Trebst suggested that the bacterial sulfate reduction pathway starting with PAPS could also be active in plants. However, my detailed studies showed that APS is the sulfur donor for assimilatory sulfate reduction in plants and also in green algae. PAPS might be the sulfur donor in lipid formation (Schwenn). For the first time, any data (those on green algae) were published by me independently of my mentor. In 1973 I left Bochum to work in Jerome Schiff's laboratory supported by a DFG grant in America. Afterwards, my scientific developments were deeply influenced by outstanding scientists such as Prof. Kandler, Munich, Prof. Trüper, Bonn, besides Prof. Schiff (Waltham). However, undoubtedly, I am extremely thankful to Professor Trebst who laid the basis of my scientific career.

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In 1965, I started my Staatsexamen experimental thesis in Professor Trebst's laboratory in Göttingen on photosynthetic electron transport in cyanobacteria with the goal of finding special evolutionary features, which could help understand photosynthetic electron transport in plants. Professor Trebst also recruited other coworkers, namely, Dr. Bernt Gerhardt, in Münster, Herbert Böhme, in Bonn and Wolfgang Lockau, Berlin, all afterwards, for this task. After nine months, Professor Trebst offered me the opportunity to continue the work as my PhD thesis. Photosynthesis in cyanobacteria and in chloroplasts turned out to be very similar, but differ by cyanobacteria's use of flavodoxin, when Fe is growth limiting, and their very active cyclic photophosphorylation with specific regulatory properties in heterocysts. Professor Trebst was a diligent mentor with regular, almost daily, discussions of my work that were always filled with progressive and helpful comments. It was fascinating to see, and to learn, how quickly he could see the weaknesses in my thoughts or experimental designs and how to improve them. In 1968, I submitted the first version of my thesis, which came back with a correction in almost every sentence. This was a disaster for me and I was about to give up. However, after several sleepless nights, I realized that Professor Trebst was right in almost all instances and that this was part of my education. In 1969, he found a postdoctoral position for me with Professor Arnon in Berkeley. Years before, Professor Trebst had been a research fellow there and had found that photosynthetic electron transport generates both "reducing power" (NADPH) and energy (ATP) required for CO_2-fixation in darkness. Meanwhile, Professor Trebst had accepted a full professorship in Bochum where he employed me on an assistantship to work mainly on N-metabolism in cyanobacteria. Again, Professor Trebst supported my efforts by regular very competent and fruitful discussions. In retrospect, I am still surprised we had only one joint publication and one co-edited book, "Biology of Inorganic Nitrogen and Sulfur." In 1975, he launched my Habilitation thesis on salt resistance in plants, which has served as the basis of my later work on plant stress. Although Professor Trebst specialized in bio/chemistry, he always supported my hobby, the ecology of plants, presumably due to the influence of his wife, a botanist. I owe almost everything in my scientific career to Professor Trebst. I am proud to have been his friend as well as his student over all the later years of his life.

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When in 1965 Achim Trebst accepted me to start a thesis and become part of his working group in Göttingen, I could not imagine all that was to come. I felt very well supported and comfortable with his knowledge, his dedication, his way of thinking and guiding not only in scientific research but also in private communication during all that time. During his early work on photosynthesis, Achim Trebst had developed a broad interest in electron transport and also CO_2 fixation in Berkeley/San Francisco and in Munich. Now in Göttingen he asked me to enter the area of CO_2 fixation in tritium water, already pioneered by work he had conducted with H. Simon and H.-D. Dorrer in Munich. Thus I became part of the team, with my workplace, however, located in a distant building at the Nikolausberger Weg, containing the Isotope Labs. H. Simon et al. had observed that even after prolonged times of photosynthesis of *Chlorella pyrenoidosa* in TOH glucose from starch was not T-labeled in C-2, in contrast to soluble hexose-phosphates. The consequent concept of intramolecular transfer of Hydrogen/T by phosphoglucose isomerase then required incubation with double labeled Glucose-1-^{14}C-2-T, Fructose-1-^{14}C-1-T_{ISO}, and Fructose-1-^{14}C-1-T_{GLU}. Procedures for the synthesis of this specific tritium labeling for the above hexoses and also for the similar pentoses in up to 500 mCurie TOH were developed. The predicted intramolecular hydrogen transfer in the isomerase reactions of hexoses and also pentoses could thereby clearly be confirmed (Dorrer et al. 1966; Fedtke 1969). One detail comes to my mind from these times of tritium measurements: Due to its very weak radiation, already in 1959 Simon et al. had developed a method based on the chemical reduction to H_2 and measurement inside the counter cell, giving a gain of some 40%. This was a very laborious procedure restricting experimentation considerably. Therefore, the arrival of a scintillation counter was a big event, and A. Trebst came to supervise all that. He took me to the side and asked me, whether 30 DM would be enough as a tip to the working men carrying the heavy counter full of lead, steel, etc. This was a lot of money for me, I admired his well doing, and of course agreed. This example shows very well how he valued every single contribution and work.

Achim Trebst personally cooperated with the Crop Protection Business at Bayer AG, with the chemists Draber and Büchel, in the field of testing new compounds at target sites in isolated thylakoids. He convinced the officials at Bayer to engage a biochemist in order to learn more of herbicide action at diverse target sites. I was lucky to become that person, including a year of further training at an American university. Trebst had arranged for me to stay a year at East Lansing in the lab of Joe Varner, which changed and determined the rest of the lives for me and my family. After that year, the study of modes of herbicide action at Bayer AG in Leverkusen and the ongoing cooperation with Achim Trebst built a successful and rewarding basis for my work (Fedtke and Trebst 1987). Danke für alles, lieber Herr Trebst.

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I first met Achim Trebst in the autumn of 1969. My Ph. D. supervisor had died suddenly and I was looking for a new job. I was offered two positions: One with the BAYER company and the other with Achim Trebst at the newly founded Ruhr-University at Bochum. So I decided to visit Bochum first and was greeted by Achim in his provisional laboratory in building NB because his promised laboratories in building ND were still under construction. I was fascinated by the aspect of working in a completely new laboratory and with the latest equipment and immediately decided for Bochum. Achim at that time worked on inhibitors of photosynthetic electron transport through photosystem II. These inhibitors are important for two reasons: (a) they allow the investigations of partial reactions of the photosynthetic electron transport chain by blocking parts of it and (b) they can serve as efficient herbicides in plant protection. Because of that Achim sought contact with the chemical industry and a fruitful cooperation with BAYER, BASF, and Schering was established. Inhibitory activity was assayed in a Warburg apparatus. Achim himself daily prepared the broken chloroplasts by grinding spinach leaves in a mortar with sand. His technician Susanne Reimer further purified the chloroplasts by differential centrifugation. Then both of them took the readings from the manometers. By the Warburg technique, three different events can be monitored simultaneously: Oxygen evolution, $NADP^+$ reduction, and ATP formation. However, not every inhibitor was automatically rendered as a herbicide. Virtually, hundreds of compounds were found to be photosystem II inhibitors but only a few of them are used as herbicides. The discovery of 2,5-dibromo-3-methyl-6-isopropyl-1,4-benzoquinone (DBMIB) together with Wilfried Draber from BAYER as the first inhibitor of the cytochrome b_6/f-complex brought Achim a citation classic. A similar type of inhibitor is the 2,4-dinitrophenyl ether of 2-iodo-4-nitro-thymol (DNP-INT), discovered by Trebst and Knoops from BAYER. Our understanding of photosystem II took a rapid progress during the last twenty years. Achim took a great part in the development of the concept that the D1/D2 protein dimer constitutes the reaction center of photosystem II when his colleagues still believed that the 47 kDa protein is the heart of photosystem II. This idea was further corroborated by the X-ray crystallography of photosystem II crystals and located the herbicide-binding site at the D1-protein. Achim was a happy person, much liked by his students, Ph. D. candidates, and coworkers.

Simon Trebst

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Beyond science my father deeply cherished his family life. Some 50 years ago, at the pinnacle of their time in Göttingen, my parents got married and embarked on their long journey together, starting out with a highly rewarding nine-month sabbatical at Purdue University in West Lafayette. It was then during one of the most productive periods of my father's scientific life—the late 1960s/early 1970s—that they settled in Bochum, built a beautiful house surrounded by a lavish garden, and grew a family of six.

My father often jokingly maintained that it was my mother, a former scientist herself, who solely raised the four of us and that he had exercised little influence on his children as he was working long hours at the institute. He was also an avid traveler who needed the frequent exchange with colleagues all around the world. Coming back home, one could literally feel the inspiration as he rushed back to the institute to bring fresh ideas to the lab. This was particularly true for his frequent trips to the US—he loved attending the Gordon Conferences, the annual meetings in Asilomar, and later in Ventura, California. You could tell how deeply he enjoyed the freewheeling American spirit whenever he was in the US—it was as if he was literally turning into his younger self embarking on new scientific directions as a postdoc in Berkeley. This was, of course, particularly true for the sabbatical in Berkeley in 1981 when he took all of us along (Fig. 11). He also kept life-long ties to Stockholm University starting with his work with the late Herrick Baltscheffsky in the mid 1960s and culminating in an honorary degree in 1990 (two more would follow from Purdue and Düsseldorf). But of all places, it was the Weizmann Institute in Rehovot that he loved most—the high-caliber scientific stimulus at the institute and the serenity of the surrounding campus were a perfect match for him. Again, it was during a sabbatical (with the late Mordhai Avron) in 1990 that my younger sister Almuth and I could witness this first hand. Besides these special places, there was one more connection that my father kept close to his heart for his entire life, his membership in the Leopoldina—the German National Academy of Sciences, to which he was admitted in 1974. For decades, he reverently attended the annual meetings in Halle which allowed him to support and keep ties with his colleagues in the former Eastern Germany.

Fig. 11 The Trebst family in Berkeley, CA (1981)

Assuming the chair in Bochum, my father realized that he had to devote himself not only to his own research, but that it has become his turn to support his junior research fellows, to seed new lines of research, and to enable the next generation to quickly grow independent. He was extremely proud of the many junior colleagues that went on to become professors in Germany and beyond. At the same time, his four children grew up and he took deep joy in the fact that all four of us went into the natural sciences (the boys into physics, the girls into medicine) and eventually obtained PhDs. Two of us have remained in academia and he was incredibly satisfied to attend our inaugural lectures as we followed in his path and assumed professor positions—Corinna at the Medizinische Hochschule Hannover and I at the University of Cologne.

As his active scientific life subsided, my father deeply enjoyed that his family once again started to grow. His first grand child was born in 2002, the eleventh in 2017. In all of us, he has deeply instilled a sense for natural beauty, the arts, and the humorous side of life.

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When Achim Trebst was appointed Professor of Plant Biochemistry at Ruhr-University Bochum (RUB) in 1967, he was the fifth professor of biology in a university that had appeared only a few years before on the architects' drawing boards. These pioneer professors were known as the "rubber boot professors" because they had to wear such boots, and helmets, when they visited the construction site of their future laboratories. My PhD advisor at the University of Munich, Meinhart Zenk, had been appointed Professor of Plant Physiology at RUB in 1968, and right after I had obtained my PhD in 1969, I was dispatched to Bochum to work as a "rubber boot assistant" and supervise the construction of our laboratory in Building ND. Here I first met Achim Trebst, when he came visiting from Göttingen, but these were rare encounters at that time. When I returned from my postdoc in 1972, research and teaching in both plant biochemistry and physiology were already in full swing.

Having been trained as a botanist and physiologist, the fundamental importance of bioenergetics became clear to me only through the interaction with Achim Trebst and his associates, and it was there that I heard first of Peter Mitchell's chemiosmotic theory of ATP generation. When Meinhart Zenk eventually decided to accept an offer from Munich, I was being considered for his succession. Achim Trebst made it clear to me, in a very frank and non-hurting way, that I was not his favorite candidate. When I was appointed after all in 1980, there was no ill feeling on either side, and we did become good colleagues. His advice to me in faculty matters was invaluable. The only return he expected was that the plant physiology gardeners would cultivate the spinach plants that he needed for his research. When I became dean, I faced the problem in the faculty meetings that colleagues far senior than myself enjoyed getting involved in legendary verbal fights, while I, as the younger and softer, was hesitant to interfere. It was usually Achim Trebst who saved the day by his intrepidity and authority, calling everybody to order.

After my move to ETH Zurich in 1987, we met only infrequently, but at such occasions it appeared that our mutual respect was increasing with distance and time. Achim Trebst was a good senior companion and advisor in a decisive time in my career.

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Generalizations are among the rewarding aspects in scientific progress, and the elucidation of the universal mechanism for electron transport-driven ATP formation is a rather recent and important example. It was Peter Mitchell's ingenious chemiosmotic theory (Nobel Prize 1978) which unified the two bioenergetics subfields, respiration and photosynthesis. It took about two decades, gradually, until the acceptance by the scientific community. The contributions of Achim Trebst and his group to this unification, textbook knowledge meanwhile, were substantial. I feel lucky and grateful, together with my colleagues, for having taken part in this fascinating time of discovery in the early seventies of last century. I had sent a long congratulating letter to Achim on the occasion of his 80th birthday in 2009. His own words of his reply seem to be adequate to me to be quoted here:

"Dear Günter,

… I have been off for my birthday. That´s why I found your congratulating letter only now. It is a welcome documentation of a successful, common time, written for us two in first place, but also for our children (which only later will become interested in the life of their elders), and also for the whole photosynthetic community (which is forgetting us). Govindjee gave up persuading me to write my life report, now you did that for an important period. I enjoyed reading it, the thoughts flew back to good memories.

The time then in Bochum was of outstanding success, the effort to apply Mitchell to thylakoids, his theory, which actually could be better proven by photosynthesis than by mitochondria. Our almost anticipating the Q-cycle, stoichiometries, pathways…

The excitement somehow ended, as you four left the group in 1975. Also afterwards we continued substantial contributions, Rolf Thauer leaving us far behind.

Of course, I remember our car ride to Syracuse/NY (after my talk at Cornell in 1969), but in contrast to you, something in my talk must not have pleased (Efraim) Racker. Later we attended together and (already) acknowledged several Gordon Conferences, and (one time) we both had no cash for a taxi to drive to Trumpower/NH (satellite meeting). Assunta (Melandri) saved us—also a wonderful meeting with great agreements…

Cordial regards,

Achim"

The four of us (Fig. 12) who left Bochum in 1975 were Hermann Bothe to Heidelberg, Erich Elstner and Ahlert Schmidt to Munich, and I to Regensburg. Trebst's review from 1974 which summarizes the fruitful early seventies, became a citation classic. Later, with the rise of molecular biology, his interest shifted to the phylogeny of photosynthetic proteins and protein complexes, in particular of quinone reduction by photosystem II and quinol oxidation by

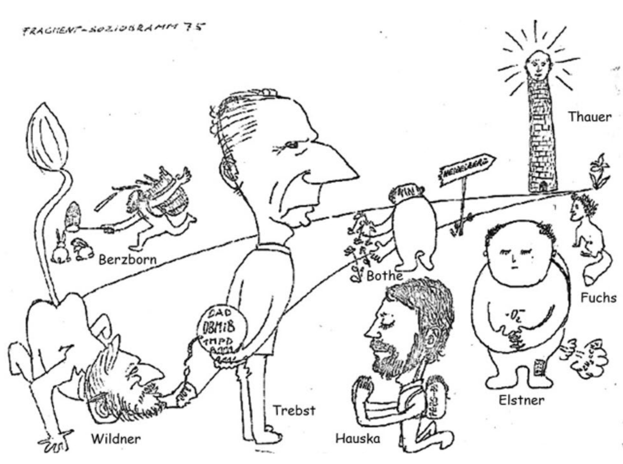

Fig. 12 A cartoonist drawing of the Bochum group

the cytochrome b_6f-complex. A visit to Bill Cramer´s group/ Purdue University in 1983 lead to another citation classic, documenting that photosynthetic cytochrome b_6 and respiratory cytochrome b share a common ancestor from some 3.5 billion years ago. His stimulating creativity as a visitor to numerous laboratories abroad was exceptional and was rewarded by multiple honorary degrees.

Certainly, a great mind passed away, and our scientific community will miss it.

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After Achim Trebst´s return in 1959 from his postdoc years with Daniel Arnon in Berkeley, he was frequently invited by German Universities to communicate newest results on the chemistry of photosynthesis. He had shown that CO_2-fixation by soluble chloroplast proteins requires NADPH and ATP, the "assimilatory power," generated by the light-gathering grana membranes.

At that time, Wilhelm Menke was teaching electron microscopy in Cologne. He concluded that the chlorophyll containing membranes must not be described as "stacks of coins," but as "piles of closed sacks," termed "thylakoids" by him. In my doctoral thesis I investigated whether proteins or lipids are exposed at their surface. Antisera against lamellar-systems, which I produced in rabbits, contained agglutinating antibodies.

To identify the reacting components, photosynthetic activity had to be tested. During my stay in Göttingen in 1965, Achim Trebst and his technician Elfriede Pistorius showed that antibodies could be isolated which inhibit NADPH-ferredoxin-oxidoreductase, CF_1 or the electron acceptor site of Photosystem I, i.e., these proteins are exposed. I ran separation columns overnight. The next morning active "broken chloroplasts" were prepared, incubated, and tested in less than 1 h. Trebst concluded that the "assimilatory power" is built up at the outer thylakoid surface. Could the orientation of the electron carriers in the membrane lead to vectorial electron transport across the membrane, from inside to outside, thus conserving energy in a H^+-gradient?

As shown by Andre Jagendorf's group in 1966, a H^+-gradient indeed enables isolated chloroplasts to generate ATP, rendering the search for chemical high-energy intermediates unnecessary. Scientific interest shifted from enzymes to membrane-embedded components.

In 1968 I was appointed as Trebst's assistant at the chair "Plant Biochemistry" of the new Ruhr-University Bochum. Since laboratories were not ready yet, I worked with Norman Bishop (Oregon State University) and Efraim Racker (Cornell University), paid by American Grants for three years. Studies with specific antibodies, done with Steve Lien, indicated that CF_1 has five different subunits, my future working subject. Günter Hauska and I localized plastocyanin inside the thylakoids.

Returning from the USA, Hauska (1970) brought Racker's concept of the "sidedness" of energy-conserving membranes to Bochum. I returned in 1971. Trebst contributed pertinent experimental work of his group with selected chemicals as inhibitors or artificial electron donors and acceptors in chloroplasts. In his review in 1974, he reorganized the puzzle pieces in the new coherent picture. Vectorial electron transport after charge separation by the reaction centers is still fundamental to understand photosynthesis.

Trebst liked to meet colleagues in the area of Bioenergetics, including Mordhy Avron in Rehovot (Israel) or William Cramer at Purdue University. In 1983 he took the sequence of an unidentified chloroplast protein, read by Reinhold Herrmann, to Purdue. There it was aligned to be a part of cytochrome *b* of mitochondrial complex III. With colored pins on paper-rolls Cramer's student William R. Widger built two helices from parts of the sequence already known. Each helix showed two conserved histidine residues on a helix-face, together suitable to hold the heme moieties in place. This significantly increased Achim Trebst's interest in model-building of protein structures using precise metal elements.

But, what influenced me most is Trebst's standard remark at coffee discussions: "Do we have an experimental approach to test our idea?"

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Being asked to contribute my reminiscence on the sad occasion of Achim Trebst's death, I would like to mention two anecdotes characterizing the exceptional personality of my mentor.

When I finished my Diploma thesis in 1978 at the Plant Biochemistry Department of the Ruhr-University Bochum under the guidance of Achim Trebst and Walter Oettmeier, Trebst gave me the opportunity to analyze certain aspects of plastoquinone function in thylakoid membranes as a topic for my PhD thesis. Trebst was highly esteemed in and closely connected with the photosynthesis community worldwide, and it was common that well-known scientists visited his department. Prof. Sane (at that time from BARC, Bhabha Atomic Research Center, Mumbai, India) was one of those visitors on sabbatical. In search for a proper project, Trebst suggested that he joins the plastoquinone project on which I had just started. This cooperation initiated a very productive time with many fruitful discussions among the three of us (myself at that time being the more listening and learning partner). It was then that I learned to value Trebst's sharp mind and outstanding ability to reconcile new data with already existing concepts. This talent enabled him later i.a. to predict the 3-D-structure of the PSII reaction center before the crystallographic analysis was finished.

Achim Trebst not only integrated current knowledge in the field of electron transport reactions but also had an instinct for technical innovations. After having attended a conference in the US he suggested to me to make use of a new device for chloroplast transformation called "particle gun," of which he had heard at the meeting. This device was basically a shotgun, which delivered tiny DNA-coated tungsten particles through the cell wall into the organelle by brute force. I politely replied that I would think about it. Inwardly, though, I considered it an odd idea, but followed his advice and established the technique. It worked beautifully (Przibilla et al. 1991), became the basis for many projects and is still an important tool for chloroplast research: a good example of Trebst's reliable sense for future trends.

Being retired now, I have met many scientists over the years, but few with an intellectual acuity, supportiveness, commitment, and friendliness like that of Achim Trebst. He was an inspiration and mentor not only to me but to many people who benefited from his scientific knowledge and experience. I will miss him.

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After finishing my diploma thesis, Achim Trebst surprisingly offered me a Ph.D. position at his Department of Biochemistry of Plants in Bochum (luckily, I was in the right place at the right time). So I became his last official doctoral student and my task was to isolate the enzymes that are involved in the hydrogen metabolism of algae. During the 3 years working in his lab, I saw Achim rarely since he traveled quite a lot at the end of his active career. However, under his supervision I had the financial and scientific liberty to set up a new anaerobic laboratory in Bochum and I successfully isolated novel hydrogenases from green algae. When I proudly handed him the first version of the introduction of my thesis, which covered 20 pages, he just said "Well written. But cut it down to four pages, please." I was surprised and also disappointed but later I realized that he was right and nowadays his statement became a kind of a winged word teaching my own Ph.D. students.

After my graduation he further supported me by finding a postdoctoral position for me in Bonn with one of his former students, Herbert Böhme, working on nitrogen fixation in filamentous cyanobacteria. In the following years, I benefited again and again from his excellent network of scientists. Anatasios Melis invited me to come to Berkeley and to do research on hydrogen metabolism again. Achim has been in Berkley in the late 1950s where he had discovered the two phases of photosynthetic reactions and later we talked a lot about this lovely place at the American West coast. My success in Berkeley enabled me to become an independent group leader and to do my Habilitation thesis.

In 2003, I got a professorship for Photobiotechnology in Bochum. I met Achim again because he still had a little office there and was very creative in giving advice and support to many colleagues on the field of photosynthesis. In the past 15 years we developed a very cordial and personal relationship (but only in English, we talked to each other by first name). He was more and more interested not only in science but also in personal things. So we talked about our families quite often and he was very proud of his children and grandchildren.

Maybe the best way to characterize the scientist Achim is to describe his probing questioning after any scientific presentation, be it in front of students at group seminars in his department or among the large international audiences at conferences. He always had a way of hitting the mark with his questions, which inexorably led into the depths of the scientific discourse. He always struggled for an adequate interpretation of scientific data; he fought hard with himself and his colleagues. But, everyone respected Achim Trebst, whether a graduate student or a Nobel laureate.

I am very thankful for all his support, interest, and stimulation on my scientific work. The world has lost a great scientist and one of its greatest minds in photosynthesis research. Moreover, a wealth of knowledge is lost. I am saying goodbye to a great human being and an incredible inspiration.

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My employment as an associate professor at the Department of Plant Biochemistry, headed by Prof. Dr. Achim Trebst at the University of Bochum, had an interesting prelude. After Prof. Dr. Rolf Thauer had left the Department for Marburg, Achim Trebst was looking for a replacement. After a first round of candidates, with which he was not quite satisfied, he asked colleagues for recommendations. He had also contacted his former coworker, Günter Hauska, who was at that time already Professor at the Institute of Botany at the University of Regensburg. Günter Hauska informed Achim Trebst about a young promising scientist at the Department of Microbiology at the University of Tübingen by the name of Karlheinz Altendorf, working in the field of Bioenergetics in Bacteria. Since Achim Trebst was reluctant to invite me directly for a seminar to Bochum—he was probably afraid of being again disappointed by the candidate—he asked Günter Hauska to invite me for a seminar to Regensburg for a "preselection procedure." Actually, I had no idea about this arrangement, but I had nevertheless a strange feeling having been invited by a "green" colleague. The day after the seminar, Günter Hauska disclosed the story to me and asked me whether I would be willing to go to Bochum for a seminar (Günter Hauska had called Achim Trebst and informed him about his positive impression). Upon my return to Tübingen, I got a phone call by Achim Trebst inviting me for a seminar to Bochum. After an intensive inspection not only by Achim Trebst, but also by Meinhard H. Zenk, Achim Trebst offered me the associate professor position, which, after a few official steps, I finally accepted. For the next 3 years, I worked with a bacterium, which from now on was called the "green *Escherichia coli*."

Achim Trebst was an inspiring mentor. I learned from him how to run, organize, and manage a department. At our mid-morning coffee meetings we had critical, but stimulating discussions, which made clear to me, how important those discussions are for the further development of science. When he disagreed with one of us, he left eventually the room by stating "I don't believe that," shaking his head in his own typical way. Achim Trebst was very generous with respect to financial support and space, which gave me the opportunity, to establish a very successful, productive, and steadily growing research group. This was the basis for obtaining a call from the University of Osnabrück for the chair in Microbiology. At the end, Achim Trebst was in a way "happy" that we left, because he was somewhat afraid that my research group would eventually "overgrow" his department.

A few years ago, Nikolaus Amrhein, Elmar Weiler, and I invited Achim Trebst for dinner in Bochum. He enjoyed this getting together very much; he felt honored by this. The happy face of Achim Trebst at this evening I will never forget; it is engraved in my memory—forever.

P.V. Sane

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After my postdoctoral research at the University of California, Berkeley, in early 1971, I wanted to learn about the research work in European laboratories. I wrote to Prof. Achim Trebst for working in his laboratory at the Ruhr-University, Bochum and to visit other labs from there. He offered me to work in his laboratory for three months and arranged for my short-term European Molecular Biology Organization (EMBO) guest scientist fellowship. I flew to Zürich (Switzerland) and after our sightseeing I took a morning train to Bochum arriving in the evening. It was a weekend and nobody would accept my US dollars as a payment in any hotel as the German Mark was to undergo revaluation from Monday. With my broken German, I could not convince the hotel managers to accept my dollars. I could finally reach Prof. Trebst after several telephone attempts. He immediately came to help me—this was the first time I met him. While taking me out for dinner he informed me that his wife had just given birth to a baby girl with the name Corinna. He gave me 200 German Marks and arranged my move to a guest house near the station from the next day, where Günter Wildner, a post doc, was also living. I was impressed by his simplicity and his concern for me—all through my stay he treated me very nicely. When I was to return to India, he told me "anytime you are in Europe do visit Bochum and if you are unable to get a job in India (it was very difficult then) you are welcome to spend more time in my laboratory." Publications arose from the work done with Günter Hauska on plastocyanin relating to its location and activity in the chloroplast membranes. Achim refused to put his name on any of our publications despite the much advice he gave us during our research. However, during my Humboldt fellowship in 1979, I was able to persuade him to be a coauthor on my work done under his guidance on proton-translocating proteins in the membranes using dicyclohexylcarbodiimide (DCCD) (Sane et al. 1979). It was an excellent experience to discuss with him our results. He was blunt in his criticism of the academic work, no matter who did or presented it.

I have enjoyed dinners at his place with my family where he offered exquisite wines. Also, he was fond of strawberries with ice-cream that were always arranged in the laboratory on his birthday on June 9. His interest in science was contagious. I met him last in 2005 when we were doing measurements on thermoluminescence with the machine I had earlier installed in his laboratory. At my departure he said "Raj you have been like a close member of my family but it seems that this is our last meeting. I wish you all the best for the future." I learnt so much from him. He commanded great respect from the scientist fraternity because of his analytical mind, simplicity, and modesty. I still cherish and fondly remember several pleasant memories of my visits and work in his laboratory.

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I first met Achim Trebst in the early 1980s in Mordhai Avron's office at the Weizmann Institute of Science in Rehovot, Israel. Achim and Mordhai were great friends. I had come to Mordhai's office to get advice about publishing the story that Autar Mattoo and I were developing about the rapidly turning over D1 protein of the photosystem II reaction center. Mordhai immediately suggested that I speak with Achim as well. I found in Achim a scientist with a wide and deep knowledge of photosynthesis and chloroplast molecular biology. We hit it off immediately.

Achim traveled widely and was known for his painstaking piecing together of information from many labs to develop the larger picture. One of his pet projects involved the structure of the PSII reaction center core, made up of the D1 and D2 proteins. His cartoon models in the later 1980s of the folded D1 protein, with its functional domains, delineated with increasing sophistication, influenced the work going on in my laboratory.

Marcel Jansen, then a doctoral student (and now Prof at University College, Cork, Ireland), was studying the effects of herbicides on the plastoquinone niche in the D1 protein. The time was January 1991; I phoned Achim, and asked him if he could, without delay, take Marcel into his laboratory for a couple of months in the wake of the first Gulf War. Achim did not hesitate; he understood the emergency and over the phone we worked out a research program that combined the interests of our two laboratories. Already on the next day, Marcel flew to Bochum (and a day later the first scud rockets fell in Israel).

Fast forward to summer 1993: After the Gulf War, Marcel returned to a quiet Rehovot after two productive months in Achim's laboratory. Following some additional work in Rehovot, a draft manuscript had been prepared which needed final polishing. I was spending the summer at Mattoo's lab at the USDA in Beltsville, Maryland. Achim, the globetrotter, was at a conference in the USA and Marcel was also in Maryland for some collaborative research. The three of us spent several days working together huddled around a tiny Model E Macintosh until the polishing was completed and the manuscript sent off for publication (Jansen et al. 1993). I remember fondly the collegiality, comradeship, and discussions—scientific and philosophical, which Achim and I conducted on that occasion.

John H. Golbeck

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I first met Prof. Trebst when I was a Ph.D. student in Anthony San Pietro's laboratory at Indiana University in the mid 1970s. What I remember best was that Prof. Trebst learned every lab member's name and that he spent time talking to every one of us to learn what we were doing and how he might be able to help. His behavior was thoroughly gracious and encouraging, yet he was tough minded, and it cemented in my mind the image of a consummate German professor. In spring 1992, Prof. Trebst learned that I was on sabbatical leave in Paul Mathis' laboratory in Saclay and he got in contact with me to ask if I was interested in giving a series of seminars around Germany. Of course I said 'yes,' and within a few weeks invitations arrived for speaking engagements in Aachen, Münster, Berlin, Regensburg, München, and Freiburg. This is where I met Dietmar Stehlik and Art van der Est, with whom I enjoy(ed) decades of exciting and fruitful collaborations. I recall perfectly my seminar in Aachen because Prof. Trebst announced after the Q&A period as we were about to close that 'Dr. Golbeck could well be a German professor,' I felt I had come full circle. However, the big fail came that evening at dinner when I absent-mindedly reached for my fork as the meal was being served. Prof. Trebst saw this and admonished my bad behavior with 'Johnny, the ladies have not yet started!' I grew up with German grandparents, and I knew exactly what I had done. Prof. Trebst was always the perfect gentleman, and this, in addition to his enormous scientific achievements, is the way I remember him.

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I first met Achim through his close collaboration and friendship with Itzhak Ohad. Achim and his wife Bärbel have had many colleagues and close friends in Israel, who they frequently visited. Itzhak was one of them. Achim's visits to Itzhak's group involved passionate and at times heated scientific debates on PSII biochemistry under photo-inhibitory conditions and were undoubtedly *the best show in Jerusalem*. My engagement in one of these discussions led to a long friendship with Achim. He was incredibly knowledgeable, especially when it involved the functions of plastoquinones in the photosynthetic electron transport and the mechanism of how herbicides inhibit PSII. In the early 1980s, Achim was unquestionably the best interpreter of data on altered herbicide-binding properties and changes in electron transfer at the Q_B level, which the newly discovered mutations in D1 had revealed. His insights and ideas enriched my group as well as the whole photosynthesis scientific community.

When the structure of the photosynthetic reaction center (RC) from purple bacteria was deciphered, Achim recognized the analogies between the L–M heterodimer from the RC with D1–D2 of PSII and, taking into account biochemical properties of the herbicide-resistance mutations, he proposed a topological model for D1 structure in the thylakoid membrane (Trebst 1986). The farsighted suggestion of five transmembrane helices, which was later confirmed by crystallographic data, together with other structure–function

Fig. 13 Trebst and Hirschberg at the Hebrew University, Jerusalem (2002)

predictions, significantly advanced research in this area by providing a framework for experimental examination. Achim's model of D1 helped my own research by suggesting potential amino acid residues of importance which we investigated by site-directed mutations. The D1 model and mode of D1 and D2 activities, proposed in the 1986 Zeitschrift für Naturforschung paper, exemplify one of the most important contributions of Achim to science. The paper has been cited more than 500 times and it is Achim's most cited publication.

Achim was already a prominent biochemist and leader in photosynthesis research when I was a newcomer in these fields. My connection and friendship with him, which developed through our mutual interests in Q_B, herbicides, and D1 structure, continued for many years after my research activities took me away from PSII into carotenoids. During that period, I enjoyed every single meeting with Achim (Fig. 13), who enriched me both scientifically and personally. Every time we met I was captivated by his enthusiasm for science, his engaging approach to younger colleagues, and his inspiring ideas, based on his profound knowledge and vast experience. I will always feel grateful for the many things I learned from him and forever be in debt to his generous and unlimited support of me, as a person, and my research.

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The first academic seminar I ever gave outside of my home institution was in Bochum, upon invitation by Achim Trebst. It must have been around 1983, while I was still a graduate student. He had read my papers and we had spoken at conferences about photosystem II components, in particular about the D1 protein, its role in binding herbicides and quinones, and how it was folded in the thylakoid membrane. I vividly remember the discussion in his office, where he had a nice scheme of the D1 protein (with each amino acid indicated and where it might sit in the membrane), based on the early-version of the hydropathy plots. With what we know now, the predicted protein-folding pattern was actually quite accurate. More excitingly, whereas everyone else in the field was thinking of the D1 protein solely in terms of binding herbicides and quinones, Achim Trebst was very early to recognize the importance of the sequence and folding parallels between the D1 protein and reaction center subunits of the reaction center from purple bacteria. It was the first time that I was exposed to this idea, and Achim Trebst, who obviously had thought about it very deeply, knew how to counter all my reservations (and there were many) regarding functional implications of such parallels between plant and purple-bacterial photosynthesis. As always, Achim was very thoughtful in his comments, and displayed an unusual breadth of knowledge in many areas. I thought to myself "if this is true, then we really have to rewrite the textbooks." In a very well cited (over 500 citations!) paper, Trebst (1986) carefully outlined the parallels between the plant and purple-bacterial reaction center systems and suggested at the end that D1 and D2 actually were the reaction center proteins of photosystem II, rather than CP47, which until then generally had been thought to harbor the photosystem II reaction center. The sequence similarity initially noted by Doug Youvan in John Hearst's group, the structure of the purple-bacterial reaction center elucidated by Deisenhofer et al. (1985), and Achim Trebst's thoughts and considerations all compellingly came together, eventually showing that the D1 and D2 proteins of photosystem II and the purple-bacterial reaction center subunits had a shared evolutionary origin and functional similarity. Achim's thoughts and ideas clearly were a step or two ahead of the others in the field. He actively encouraged others to try to prove or disprove his hypotheses experimentally, and in the mid- to late-eighties this was a very active and fertile research field. In the end, indeed, Trebst's hypotheses proved to be correct.

Fast forward to 1999–2000, when I had the privilege to be on sabbatical in Bochum. Achim Trebst had retired but still came regularly to the Department, where he kept an office and had a small research operation; he attended seminars, wrote, and shared his thoughts and wisdom with students and others. He then, as always, was a pleasure to exchange thoughts with. There was no such thing as scientific heresy for him, and he was always open to unconventional ideas and interpretations, as long as they fitted the data. Also, from a personal perspective it was a great pleasure to be invited for dinner and experience his thoughtful and caring personality also away from the lab. Achim picked us (and our extensive luggage) up from the airport when we arrived for our sabbatical, and our oldest son Josh still has a functional Maerklin model locomotive that Achim gave him when he found out that he was interested in trains. I am very thankful to have known Achim, a great scientist and a very good person.

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I first met Achim in 1969 shortly after I had assumed my faculty position at Purdue University. Achim came to Purdue to work with Fred Crane, who was the world expert on the properties of the lipid-soluble ubi- and plastoquinones. I recall that I was sitting at my lab bench running a redox titration of the fluorescent yield of a photosynthetic bacterium when Achim came to introduce himself. We met frequently, both over scientific discussions and socially, over the next half year during Achim's sabbatical. Our last mutual adventure was helping Achim avoid a penurious last rent payment at his apartment complex when he left Purdue.

I visited Bochum in 1974–1975 when I was on sabbatical in Amsterdam. I recall that it was an extremely stimulating atmosphere, which was to present a seminar on the question of various aspects of cytochrome function. The questions and discussion were relevant and stimulating.

During the late 1970s and early mid 1980s, Achim would visit us in West Lafayette as part of his trips to the US for a Gordon Conference or some other event. It was in the summer of 1983, at the time when protein sequences of membrane proteins have become known, that he came collaborated with Bill Widger and I on an examination of the amino acid sequences of the *b* cytochrome component in the cytochrome bc_1 and b_6f complexes. In the spring of 1984, we presented in the PNAS a comparison of the distribution of hydrophobicity in the cytochrome *b* subunit from five different mitochondrial sources and cytochrome b_6 from spinach. Using the Kyte–Doolittle values for relative hydrophobicity of the amino acids, it was found that the distribution of hydrophobicity, the "hydropathy" function, was almost identical between the different mitochondrial *b* cytochrome polypeptides and cytochrome b_6. Thus, the mitochondrial *b* cytochrome peptide was predicted to have eight transmembrane (TM) helices with conserved opposing histidine residues on helices II and IV, thus defining the heme position on apparent sides of the cytochrome in a polypeptide that contains eight TM helices. A homologous arrangement was found for a smaller (4 TM helices) cyt *b* ("b_6") functioning in oxygenic photosynthesis. Isolated Cyt b_6 also contains a three TM membrane protein that corresponds to the C-terminal three helices of the eight TM helix cytochrome *b*. One may say that this study was fundamental for subsequent structure-based discussions of the pathway of electron transfer in cytochrome b_6f and bc_1 complexes. It was fitting that the PNAS manuscript on these studies should have been reviewed by Warren Butler, although it was his last.

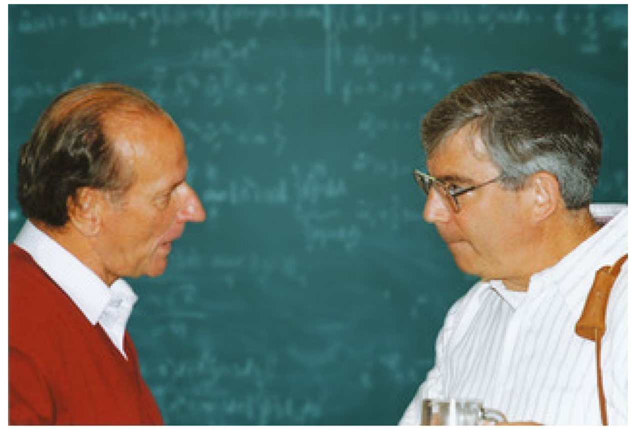

Fig. 14 Trebst and William A. Cramer at Purdue University (2001)

Achim told me that he liked very much to work in the Lilly Hall Life Sciences where our laboratory was situated. One day, I also found him in the library on the third floor of the building. He told me that he particularly liked to work there reeling among the many shelves of books and looking down at the students walking back and forth to their courses (Fig. 14).

Scientifically, the 1983 visit to Purdue by Achim was the most exciting in terms of consequences for our understanding of photosynthetic energy transduction. A few years later, Achim came to Purdue to receive an honorary Ph.D. degree, awarded for his contributions to our understanding of the molecular basis of photosynthesis.

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I first realized "Achim Trebst" as one of the leading figures of photosynthesis when I was student of biology at Tübingen University: His review "Energy conservation in photosynthetic electron transport of chloroplasts" (Trebst 1974) made me really interested in photosynthesis and was decisive for my decision to focus on this topic. I then joined the group of Prof. Witt at TU Berlin and came to know Achim Trebst personally as postdoc in this group around 1985. We were expecting Achim Trebst as reviewer for our SFB grant application (Collaborative Research Center funded by DFG) on water-splitting photosynthesis and from the increasing tension in the group I could estimate the respect for and even

Fig. 15 At the farewell party of Brigitte Depka with Matthias Rögner and Thomas Happe (2011)

the fear of Achim Trebst. Indeed, his questions on our project came quickly and directly to the critical points and he disclosed problems mercilessly—nevertheless also giving valuable pieces of advice, especially to young researchers like me. His particular talent for in-depth investigations was the reason for his nickname "the detective" in the Berlin group. That time I would never have dreamt that—about 11 years later—I would take over his chair at the Ruhr-University Bochum. When this happened, Achim Trebst still had a small office and lab at the chair and participated with a small project in the photosynthetic research activities. For many years he was contributing with excellent ideas to the progress of our projects and especially he was always open with advices for the young researchers of my team. This way, he practiced, indeed, what is now introduced as "senior professorship" in German universities, i.e., experienced professors who contribute actively to scientific progress after their retirement: For Achim Trebst this was a matter of course. Legendary was his metal cabinet filled with reprints—both historic and up-to-date ones: When challenged with new ideas, he often went to this cabinet, digged out some older reprints and could show that such ideas had been tackled or even solved a long time ago. This was sometimes like a shame or a defeat for us, especially as he did not need a computer for this—it was all in his brilliantly working brain (he would also be the only one to find inhibitors and other stuff from his experiments hidden somewhere in freezers….). For several years after his retirement he still routinely attended seminars of the faculty and the chair, especially enjoying visits of invited foreign speakers. Characteristically, in the discussion session after the talk he would be one of the last to ask a question, and typically this was the most challenging question for the speaker, showing that he unmasked once again the most critical point of the presentation. Besides, Achim also contributed many interesting stories on the history of photosynthesis which he experienced in his wide personal network and which had serious and sometimes also funny backgrounds (Fig. 15). Unfortunately, all these stories are gone now and we miss Achim's helpful advice, his wisdom, and his humor very much!

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Achim Trebst was a well-known specialist on photoinhibition of photosystem II, turnover of the D1 protein and singlet oxygen quenchers/scavengers such as carotene and tocopherol when we started to discuss intensively. He was interested in $^1O_2$ as one of the signals relaying the state of the electron transport pathway to the gene expression system. In this respect, he was interested in our work on the midpoint potential of the primary quinone acceptor of PSII, Q_A, which acts as a molecular switch altering the pathway of charge recombination between P_{680}^+ and Q_A^- (Trebst and Krieger-Liszkay 2006; Krieger-Liszkay et al. 2008). This recombination reaction takes place either indirectly *via* the back reaction of the primary charge pair ($P_{680}^+Pheo^-$) leading to a high yield of P_{680} triplet or alternatively, depending on the midpoint potential of Q_A/Q_A^-, directly to the P_{680} ground state. $^3P_{680}$ reacts with $^3O_2$ generating $^1O_2$. Inhibitors in the Q_B site shift the potential of Q_A and modify thereby the yield of $^1O_2$ generation.

In the earlier years of 2000, Beat Fischer, ETH Zürich, worked on photooxidative stress responses and changes in gene expression levels in *Chlamydomonas reinhardtii*. Fischer demonstrated that the glutathione peroxidase gene *gpxh* was specifically upregulated by singlet oxygen. Together with Achim Trebst, he and I showed that the expression of *gpxh* was, indeed, controlled by $^1O_2$ arising from PSII. Our submitted manuscript came back with the comment, by a most likely young reviewer, that a loading control was missing for the immunoblot. The blot had been done in Bochum by Brigitte Depka. Achim Trebst was outraged because he had never done a loading control in his life. In Freiburg, I employed a student for 3 weeks who repeated the blot, now with loading control. In addition to this original work, Achim Trebst invited me to write two reviews on $^1O_2$, photoinhibition, and protection by tocopherol, where the second one happened to be his last publication.

I appreciated scientific discussions with Achim Trebst (Fig. 16), his interest in our work, and his encouragement. I was touched when he said to me "Sie können auch Achim zu mir sagen" (you can call me Achim), not that I had dared to do so. Nowadays, we remember him when we open the freezer here in Saclay and find yellow stained envelopes with chemicals, a piece of paper with

Fig. 16 Achim Trebst at home (2014)

the chemical structure and his words "this you can also try once, Achim." What will we do when we run out of DNP-INT?

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