A personal review of 50 fruitful years of research in the sulfur field - Prof. Dr. Ahlert Schmidt (1940-2025)

The following text is based on a version written by Prof. Dr. Ahlert Schmidt in 2015 and slightly adapted by Jutta Papenbrock in 2025.

Ahlert Schmidt was born in 1940. After completing his Abitur in 1961 in Bremen-Vegesack, he was required to serve in the military for 12 months. However, with the construction of the Berlin Wall, this term was extended to 18 months, and he eventually left service as a reserve officer (Leutnant der Reserve).

His academic journey began at the University of Göttingen in the winter term of 1962/63, where he embarked on studies in biology. During the first two years, he completed introductory courses in botany and zoology, alongside necessary lectures in chemistry, including inorganic, organic, and analytical chemistry, as well as physics. By the end of his fourth semester, he had completed all requisite chemistry courses for a biology student.

In his fifth semester, he became part of the "Botanisches Institut" at Göttingen, led by Prof. Pirson. Here, he learned about analytical enzyme measurements and studied plant regulation by light intensity and different wavelengths, particularly the effects of red light. Under the guidance of Prof. Trebst, he received training on measuring chloroplast electron transport rates. Excelling in his final examination, he was offered the opportunity by Prof. Trebst to join his research group to pursue a PhD. Despite his initial aspirations to become the Director of the Institute for Beekeeping at Celle, and with guidance from his family during a time of personal loss, he accepted the offer.

April 1965 became a pivotal month in his life. His brother Klaus and his father both passed away, while he also became engaged to Margarethe von Wrangell. Amidst these life-altering events, he decided together with his family to start his PhD work at the Botanical Institute of Göttingen under Prof. Trebst's mentorship, setting the stage for a career-defining journey in biochemical research.

Reflecting on the past 50 years, he acknowledges how dramatically his life changed, yet ultimately for the better. On May 2, 1965, he returned to Göttingen and accepted Prof. Trebst's offer, eager to discuss the direction of his research. Prof. Trebst suggested exploring the role of chloroplasts in sulfur metabolism and encouraged a combination of studies in biochemistry, botany, and microbiology, the latter under Prof. Schlegel, for his thesis defense.

Diving into the topic, he spent three weeks meticulously studying sulfate reduction in plants and microorganisms. He proposed starting with measuring ATP sulfurylase, by setting up his lab space, ordering necessary chemicals, and self-teaching the analysis of sulfur metabolism enzymes. Despite his initial struggles with Prof. Trebst's lectures on photosynthesis, he dedicated himself to learning biochemistry, using textbooks by Mahler and Cordes, and Karlson, to supplement his understanding. By 1966, he had mastered the concepts presented in the lectures by Prof. Trebst.

The introduction and courses in microbiology by Prof. Schlegel greatly interested a scientist, and the knowledge acquired in microbiology at Göttingen proved immensely beneficial throughout his life. In the laboratory setting, colleagues mastered isolating intact chloroplasts capable of fixing CO_2. They provided the surplus chloroplasts to Ahlert Schmidt to investigate the presence of his ATP sulfurylase enzyme. The measurements yielded exciting results, indicating the enzyme's specific activity. Prof. Trebst was delighted with these results and proposed a "yes or no" experiment to further validate the findings.

The suggested experiment entailed using isolated chloroplasts incubated with radioactive sulfate to determine if radioactive cysteine was formed. To achieve this, analytical methods for the chromatography of cysteine were prepared using paper chromatography, seeking liquid mixtures that could effectively separate cysteine, sulfate, and other metabolic intermediates. After separation, a radiographic film was placed over the chromatographed paper to visualize the results.

By February 1967, the techniques to separate the desired products were successfully developed. An experiment involving isolated chloroplasts exposed to radioactive sulfate was conducted. This mixture was briefly heated before being applied to paper chromatography. Once the paper was developed and dried, a radiographic film was placed over it. After sufficient exposure time, the radiographic film was developed, and non-labeled amino acids were visualized using protein techniques.

This inaugural experiment confirmed the formation of radioactive cysteine, providing incontrovertible evidence that chloroplasts can reduce sulfate to cysteine. This significant experiment took place in February 1968. Ahlert Schmidt was the first to demonstrate experimentally that plant chloroplasts have the capability to synthesize cysteine from sulfate. With these results, the primary question of his thesis was affirmatively addressed: "Yes, they can."

He could demonstrate the presence of labelled APS and PAPS as intermediates formed and he could find labeled sulfite if sulfate was added and labeled H_2S if non-labelled H_2S was added. The kinetics for these intermediates were measured, adding substantial detail to the research findings. By summer 1968, he had gathered sufficient evidence to conclusively show that chloroplasts possessed the full suite of enzymes for sulfur reduction.

Subsequently, he completed his thesis, titled "Untersuchungen zur assimilatorischen Sulfatreduktion isolierter Chloroplasten," which was accepted in late autumn 1968. He defended it successfully in February 1969 at the end of the winter term.

When Prof. Trebst received an offer for a Plant Biochemistry chair at the newly established Ruhr-Universität Bochum, he invited his protégé to join the transition. Moving to Bochum in April 1969 with his family, including newborn daughter Elisabeth, he helped establish the new Institute for Plant Biochemistry, organizing equipment for the forthcoming academic year.

During this period, he critically examined the presence of sulfur nucleotides APS and PAPS, both labeled within chloroplasts by radioactive sulfate. He suspected that the *Escherichia coli* sulfate reduction model via PAPS might not apply to plants. Using newly developed thin-layer

chromatography with a fluorescence detector it was possible to separate APS and PAPS very clearly. However, he never found PAP as an end product of the reaction.

His hypothesis was that if evolutionary processes had enabled an ATP kinase with a low K_m to phosphorylate APS to PAPS, it should also be possible to develop a reductase with a low K_m towards APS, challenging existing assumptions about plant sulfur metabolism.

He observed that a PAPS-nucleotide was not formed when using arsenate, despite measurable ATP sulfurylase activity with arsenate. The APS analogues with arsenate or molybdate had notably short lifetimes due to rapid autohydrolysis, which was inconsistent as an intermediate. Intrigued, he questioned whether plants might follow an APS reduction pathway rather than the PAPS reduction pathway identified in *Escherichia coli*.

Prof. Trebst, although initially skeptical, allowed him to investigate this possibility in detail as his assistant. He embarked on preparing radioactive-labeled APS and PAPS, conducting enzyme assays to assess the activity of these sulfur-nucleotides in cell-free systems. His experiments were carried out in parallel using extracts from both spinach chloroplasts and *Chlorella* extracts.

He analyzed if either AMP or PAP formed as end products could inhibit the reaction. Additionally, he explored interactions with labeled and unlabeled APS and PAPS. From these meticulous experiments, he gathered definitive evidence that APS served as the sulfur donor for reduction, with no requirement for intermediate PAPS formation in the conversion of APS to sulfite.

When presenting these findings in a lab meeting, he faced critical feedback from Prof. Trebst, who found the notion of plants differing from bacterial processes unsettling. When discussing publishing the data, Prof. Trebst declined co-authorship, suggesting he publish independently if he was confident in his conclusions.

Undeterred, he proceeded to publish his work alone, confident in the accuracy of his findings (https://doi.org/10.1515/znb-1972-0214). His groundbreaking discovery that APS was indeed the sulfur donor in plant sulfate reduction sparked a controversy regarding the uniqueness of plant metabolic pathways compared to those of bacteria. This debate was not conclusively resolved until genetic methods became available several decades later, ultimately affirming his pioneering insights.

He pondered why evolution favored the APS-dependent pathway in plants rather than the bacterial PAPS-dependent pathway. His hypothesis was that plant metabolism, distinct from bacterial systems, might use PAPS sulfation for regulating developmental signals. Recent publications have confirmed this, finding sulfotransferases in plants that sulfate specific metabolites by using PAPS, indicating a regulatory role.

The controversy surrounding his findings concluded in 1997 when Tom Leustek contacted him about using bacterial mutants deficient in sulfate reduction to screen for plant enzymes. Because he hadn't worked on the enzyme for some time, he encouraged Leustek to proceed, leading to findings presented on a sulfur meeting in England. Genetic data eventually validated his APS-

dependent pathway theory, confirming his original work was correct despite earlier doubts and conflicting data from Prof. Trebst's laboratory.

During his time in Bochum, he also explored reducing sulfur nucleotides to sulfide. He demonstrated that APS could be directly reduced to H_2S in plant extracts using ferredoxin, which is reducible by ferredoxin-NADP reductase when coupled with an NADPH-regenerating system. This revealed a protein-bound intermediate capable of further reduction to H_2S, with data meticulously recorded in his notebooks.

His experiments revealed that while plant extracts interacting with sulfite and methyl-viologen as reductants initiated reduction (indicated by bleaching of the solution), very little H_2S formed. This led to discovering thiosulfate formation, suggesting a protein-mediated reaction not involving external sulfite supply. From these observations, he theorized the involvement of siroheme and proposed that free sulfite might displace siroheme-bound sulfide, thereby forming thiosulfate. This encapsulated the principle of reducing dithionite to thiosulfate, contributing valuable insights into enzymatic pathways involved in sulfur metabolism.

Ahlert Schmidt left Bochum in the summer of 1972 to spend 18 months in the lab of the late Jerome Schiff. Prior to moving to the United States, he ensured the publication of his APS sulfate reduction findings. In Schiff's lab, he worked on algal mutants blocked in assimilatory sulfate reduction. He developed a method to extract active proteins from algae, which could then be lyophilized and stored for months without activity loss. These extracts enabled the mixing of different mutant extracts to assess complete reduction pathways in vitro and to complement the pathway with extracts from algae mutants in sulfur metabolism.

He also revisited his observations on labeled proteins from Bochum by preparing radioactive S-sulfoglutathione from oxidized glutathione (GSSG) and free labeled sulfite. He used lyophilized *Chlorella* proteins to find protein-bound sulfite, which he successfully identified. By heating an extract incubated with labeled sulfoglutathione, he isolated a low-molecular-weight compound through paper electrophoresis. This compound, found in a "yellow fraction" with high mobility, released sulfite particularly under alkaline conditions, suggesting an iron-bound sulfite rather than a thiol-bound one. He recognized that sulfide binding to iron heme-proteins in the respiratory chain could be toxic.

Jerome Schiff, however, was not interested in these findings. The work on low-molecular products labeled by sulfite remained unpublished, but he took his valuable notebooks with him when he left the lab. At the conclusion of his time in Schiff's lab, he received an invitation from Prof. Kandler to join the Botanical Institute of the University of München as a coworker starting January 1, 1974, and he completed his habilitation there in the summer of 1974.

His time at the University of München was devoted to further research on sulfur metabolism. He focused on green algae and later cyanobacteria, aiming to understand why plants evolved to utilize the APS sulfate reduction pathway.

He believed that sulfur is transferred by the sulfate activation system to the siroheme of the sulfite reductase. His ongoing hypothesis is that the activated sulfate is first transferred to a thiol group, then passed to the siroheme of the sulfite reductase. The addition of an electron to

the siroheme-bound sulfate frees the thiol group and results in a siroheme-bound sulfite, which is further reduced to a siroheme-bound H_2S. This bound sulfide can be transferred to a thiol group by a sulfurtransferase, directing it into the cysteine synthase or other biosynthetic pathways requiring reduced sulfur. His detailed analysis from 1969 to 1972 at Bochum indicated that surplus sulfite could result in thiosulfate through thiolytic cleavage of the bound sulfide.

In Munich, from 1974 to 1988, he revisited the APS-PAPS topic, partly influenced by Roger Stanier, a renowned microbiologist who invited him to the Pasteur Institute in Paris. Stanier was curious about the role of sulfur metabolism in differentiating cyanobacteria. Curious if cyanobacteria mirrored plants' or *Escherichia coli*'s sulfate reduction pathways, Ahlert Schmidt frequently visited Paris to collaborate with Stanier, leveraging his microbiology background.

He discovered that there are some strains which use APS for assimilator sulfate reduction and some strains using PAPS for assimilatory sulfate reduction – so for the development of higher plants the APS system was preferred.

At the University of München's Botanical Garden, he analyzed APS-sulfotransferase activity in approximately 30 plant species to verify its role in sulfate reduction. He wondered about its regulation concerning sulfur forms available to plants. Collaborating with Prof. Erismann and Dr. Brunold at the University of Bern, he investigated if the APS-sulfotransferase pathway in Lemna minor was affected by atmospheric H_2S as the sole sulfur source. Their experiments showed that H_2S application downregulated APS-sulfotransferase activity, highlighting that H_2S was preferentially used for plant growth. This evidenced that APS-sulfotransferase was integral to in vivo sulfate reduction, reaffirming the APS-dependent pathway's role over PAPS.

To explore sulfate reduction in bacteria, he collaborated with Prof. Trüper at the University of Bonn's Institute of Microbiology. Prof. Trüper focused on sulfur oxidation in *Thiobacillus* and one intermediate in energy conversion was the sulfur nucleotide APS, which exchanged the sulfur of APS with a phosphate to from ADP gaining energy this way. This strain could grow also on sulfate as sulfur donor. So they analyzed this strain and also other phototrophic bacteria for an assimilatory APS-reduction system and for use of either APS or PAPS for sulfate reduction.

His time in Munich was marked by discoveries involving thioredoxins, revealing their role in activating proteins across a wide spectrum of organisms, including bacteria, cyanobacteria, algae, plants, and even humans. Collaborating with Prof. Follmann in Marburg, they showed thioredoxins from different sources were interchangeable in vitro, with thioredoxin-dependent reactions activating proteins like Glutathione reductase and Fructose-bisphosphatase. This demonstrated thiol activation as a regular process for transitioning chloroplasts from dark to light conditions.

In 1982, he had the opportunity to present his insights into sulfate reduction pathways at the New York Academy of Science, later published in Jerome Schiff's edited volume "On the Origin of Chloroplasts."

His creative tenure in Munich preceded a move to Hannover, where he became a full professor at the Tierärztliche Hochschule (TiHo). There, he taught veterinary students about crop and toxic plants, engaged with environmental issues, water ecology, and sulfur nutrition, but could not delve deeply into sulfur genetics due to resource constraints.

Faced with institutional restructuring in Niedersachsen that threatened his botanical institute at TiHo, he advocated successfully for the Chair at the University of Hannover, aligning with his research goals. This position allowed him to integrate plant genetics into his research. He recruited Jutta Papenbrock, a newly graduated PhD in plant molecular biology, to study sulfurtransferase genes. Capitalizing on his earlier work on thiosulfate reductases, they explored genetic links between sulfurtransferases and cysteine biosynthesis.

His investigations in Hannover built on past observations of thiosulfate formation using sulfite reductase assays from his Bochum days. He analyzed cysteine synthase's ability to utilize different thiols as "cysteine-equivalent" amino acids, validating that the enzyme accepted various thiols like mercaptoethanol and DTE. These findings highlighted the enzyme's flexibility, confirming that cysteine synthase is not specifically reliant on H_2S but can incorporate other protein-bound sulfides for cysteine synthesis.

He has gathered evidence supporting the possible cleavage of a siroheme-bound sulfide by a thiol group, subsequently transferring the sulfide to cysteine synthase without generating free H_2S. While he acknowledges that plants can emit H_2S under certain conditions, and he has coauthored papers on this phenomenon, he remains open to alternative explanations and approaches to this biochemical process.

Retired for a decade (in 2015 when this manuscript was written), he reviews the field from the confines of his home computer, with limited access to the latest literature. His perspectives remain rooted in experimental data he collected over his research career, much of which remains unpublished.

Reflecting on his 50-year scientific journey, he expresses deep satisfaction with his work in sulfur metabolism and related areas. He considers himself fortunate to have pursued research topics of personal interest and identifies his 15 years at the University of München (from 1974 to 1988) as the most thrilling phase of his career. The period from 1997 to 2005 at the University of Hannover stands as a close second, highlighted by the validation of his early work on assimilatory sulfate reduction. He takes pride in seeing a younger generation of scientists building on his foundational research, aided by modern genetic methodologies, revitalizing efforts to understand plant growth and its ties to sulfur metabolism. This overview encapsulates his dedication and passion for his field over 50 years, underscoring a lifelong commitment to advancing scientific knowledge.

The sulfur community: On the occasion of the retirement of Prof. Dr. Ahlert Schmidt the Institute of Botany at the University of Hanover invited to a scientific colloquium “40 Years of Sulfur Research” on June 17 and 18, 2005. Ahlert Schmidt and his wife Margarethe Schmidt are in the first row on the left. Picture: private.

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