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Obituary

August Ried (1924–2004), an outstanding researcher, an artist and a dear friend*

A 1975 photograph of August Ried

August was born on 17 July 1924, at Landshut, a town in lower Bavaria, Germany. Having entered school after his parents August Ried (1890–1975) and Anny Ried (maiden name: Moertlbauer) (1885–1966) moved to Frankfurt, August, still a high-school student, was called up to serve as a soldier in 1943. After World War II, he completed high school and enrolled as a student of biology at the University of Frankfurt. Specializing in botany, he began a doctoral thesis on comparative stress physiology of lichens covering the rocky banks of mountain creeks. His supervisor, Camill Montfort, was a brilliant and inspiring ecophysiologist of his time. After having received his doctoral degree in 1953, August became Montfort's assistant, qualified as lecturer in 1958 and became Professor of Plant Physiology in 1965. During 1972–1973, he served as Dean of the Biological Faculty at Frankfurt University where he stayed until his retirement in 1988.

In 1952, August married his fellow-student Isolde Felgner, a gifted ecologist; they had two sons (Holger, born in 1954 and Gunthard, born in 1956) and two daughters (Ingunn, born in 1959; Joerdis, born in 1967). They moved in 1975, from Frankfurt to a rural area in the Taunus hills, northwest of Frankfurt where they enjoyed living close to nature. August was very proud of the beautiful garden that he had designed and maintained.

After having become an acknowledged expert in the identification of lichens, August devoted himself to the ecology of lichens. In every season of the year, he traveled towards a suitable region, carrying in his backpack rubber boots, hammers and chisels. After taking photos for later mapping, he chiselled off hand-sized pieces of rocks covered

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with lichens to take them to his laboratory. There he measured photosynthesis and respiration of numerous species that were first desiccated and then re-watered. He found that the cause for the *zonation* of lichens in littorals was their specific intrinsic tolerance to desiccation or submersion. Together with Isolde, and his supervisor Montfort, he completed earlier studies on ecotypes of marine algae in the littoral of the Baltic Sea and the North Sea by analyzing the effects of elevated temperatures (up to 37 °C) on photosynthesis. The different species sampled from the same spot differed substantially in their heat tolerance. Hence, temperature tolerance of algae also depended much more on the genotypic constitution than on habitat conditions. Such results were new and exciting in the early 1950s.

With one of us (CJS), who had just finished his doctoral thesis, August worked on the respiration of the *Chlorella* strain SAG 211-8b. CJS and August established highly synchronous cultures by employing light:dark cycles of 16:8 h. During the life cycle of the cells, respiration rates changed considerably reaching a maximum at completion of cell division (Ried et al. 1963). At that stage, respiration was most sensitive to cyanide (inhibition $>80\%$) and could not be stimulated by externally added glucose. The respiration of young cells harvested about 5 h later, on the other hand, was minimal and was inhibited by cyanide by less than 20%. At the same time, however, respiration could be strongly boosted by glucose and this extra respiration was again highly sensitive towards cyanide. This result disproved Otto Warburg's hypothesis that intracellular and extracellular substrates were metabolized by different routes, and August received a hand-written letter of congratulations from Sir Hans Krebs.

In the early 1960s, August entered the field of photosynthesis. In C. Stacy French's laboratory at the Carnegie Institute of Washington at Stanford (California), he analyzed transient changes in the rates of oxygen exchange of *Chlorella* cells following short light pulses (Ried 1968). He identified distinct, reproducible transients and investigated their significance. Exposure of juvenile cells to short light flashes resulted in a rapid initial oxygen burst (T_1) followed by a slower, likewise positive oxygen exchange in the subsequent dark (T_3) which, however, indicated the vanishing inhibition of respiration by photosynthesis, the basis of the so-called *Kok effect* (see Rabinowitch 1951, pp. 1113–1117). For T_1, August found a photosystem (PS) II action spectrum in agreement with other authors, whereas T_3 showed a pure PS I action spectrum. Thus these two transients allowed August to analyze separately PS I and PS II action spectra in the same light flash, a marvellous experimental result. These action spectra (Ried 1972) are of a quality, resolution and reliability that has never been obtained. In the 1970s, August met Ivan Šetlík from Třeboň, Czechoslovakia, a well-known photosynthesis researcher from behind the then so-called iron curtain. The two scientists who had similar research interests, started a fruitful collaboration and published several papers of which one stands out: August had interpreted the inhibition of respiration by PS I light (see above) as being caused by cyclic photophosphorylation. Exhaustion of the cellular ADP pool due to cyclic ATP formation was thought to inhibit respiration in a Pasteur effect-like mode. Ried and Šetlík were able to verify this hypothesis by simultaneous analysis of oxygen exchange and internal adenine nucleotide concentrations (Ried et al. 1973).

August devoted the last two decades of his professional life to photosynthetic energy distribution in marine red algae. This work is probably the most important one of all his research work on photosynthesis. As a guest of the *Station Biologique* in Roscoff, France, he collected many species of red algae which he was able to keep alive for months in his laboratory while conducting the experiments. Owing to the specific properties of their light-harvesting systems, red algae turned out to be ideal organisms to investigate the so-called *state transitions*. In algae, the regulation of energy distribution between the two photosystems is of eminent ecological significance, especially in coastal habitats where the actual light climate changes with the tides. By extensive studies, August found that the radiation energy absorbed by the phycobilins equilibrates between PS I and PS II (Ried et al. 1977). The most interesting result, however, was that the state transitions were light-dependent in both directions. The transition from state 2 to state 1 depended on PS I light, whereas the reverse transition depended on PS II light (Ried and Reinhardt 1977). August's absolutely logical conclusion was that the redox state of an electron carrier between the two photosystems must control the energy distribution (Ried and Reinhardt 1980). This idea was new and now we know that he was right. It is the redox state of plastoquinone/plastoquinol that exerts the control and processes like phosphorylation/dephosphorylation of thylakoid proteins are involved, too, at least in chlorophyll $a+b$ plants (Allen 2002). In red algae, this question is still open.

In his photosynthesis experiments, August preferred to employ classical non-invasive physiological techniques: gas exchange and chlorophyll fluorescence. Through extensive experimentation and analytical thinking, August arrived at amazingly detailed mechanistic conclusions. August had a special ability to comprehend complex physiological problems and he knew how to design the right experiments. He was able to concentrate on the problems so deeply that he often neglected the world around him. Once we saw him knocking at his own door, listening for the *come in* – until he suddenly realized where he was. His papers were highly intellectual and precise; sometimes, he was so concise that it was difficult to understand him. Likewise challenging were his oral presentations. He supposed everybody knew and understood as much as he did. The students suffered in his lectures: while they had scarcely understood the basics, August explained to them the latest results from the literature. Among them he was considered as too demanding, therefore only a few students dared to request him to be their advisor for a diploma or doctoral thesis. But those who joined him got to know a different person: always ready to answer any question, but never asking embarrassing questions by himself, never exerting pressure, always patient and kind.

August was a reserved, modest man; he ran a small laboratory with a small budget, a technician and a few students; and he refused to fight for his own benefit. Much of the experimental work, he published, was done by his own hands. August was a broadly learned, educated and cultured man, who had a great talent in fine arts that he had inherited from his mother; she was an excellent amateur painter. When he retired in 1988, he was finally free to devote himself to painting while listening at full blast to classical modern music, especially by Stravinsky. His expressive pictures display in a unique way the interactions between living beings and their environments, also in a spiritual sense. Though being an ingenious and skilled artist, August never let his paintings to be shown to the public.

August overcame two severe heart attacks. In summer 2001, however, he suffered a stroke, from which he never recovered. Needing care, he was tenderly supported by his wife and children. He passed away on 9 February 2004, almost 80 years old. The scientific community has lost an excellent researcher, esteemed colleague and a dear friend.

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