

# Horst Tobias Witt (1922-2007)

Seminal research on photosynthesis.

During the second half of the twentieth century, great strides were made in revealing the molecular details of oxygen-generating photosynthesis, the basis of almost all life on Earth. Horst Witt was one of the prime movers behind this revolution in understanding.

Witt was born in 1922 in Bremen, Germany. From his youth he was interested in physics, and while at school he won a prestigious prize for his high-risk, and literally explosive, experiments on supersonic airfoils. On the outbreak of the Second World War, he entered the Luftwaffe, but his scientific aptitude led to his early (and lucky) release to take up research at the University of Göttingen. He received his PhD in solid-state physics in 1950, and then moved to the Max Planck Institute of Physical Chemistry where — like several other brilliant young scientists, including Manfred Eigen — he began to explore the largely hidden beauties of the molecular life sciences.

Witt chose oxygenic photosynthesis as his lifelong research topic. Inspired by the methods pioneered by George Porter and Ronald Norrish, he embarked on work with the technique of flash spectrophotometry. Using algae, in 1955 he discovered reactions of chlorophylls, carotenoids and cytochromes that occurred in microseconds. By 1961, his work, along with the independent discoveries of Lou Duysens and of Bessel Kok, led to a scheme with two photochemical reaction centres in series. At photosystem II, electrons are removed from water, generating a strong oxidant, oxygen. At photosystem I, the electrons are used to produce a strong reductant, NADPH (and thence sugars). The energy difference between the strong oxidant and the strong reductant powers all oxygen-based life.

At that time the two Nobel laureates in the field, biochemist Otto Warburg and spectroscopist James Frank, were fighting their famous battles from ensconced positions. When confronted with Witt's detailed reaction scheme in 1962, Warburg mused: "Could you tell us how the chemical mechanism of photosynthesis can be described on the basis of your spectroscopic observations?" Witt countered with a well-aimed jibe at his eminent critic, the pioneer of oxygen detection, by observing that "it would be difficult to deduce the mechanism of a combustion engine based only on sniffing the exhaust".

In 1962, Witt moved to the Technical University of Berlin, where he moulded the Max-Volmer-Institute for Physical Chemistry into an internationally renowned laboratory for biophysical studies of photosynthesis. The

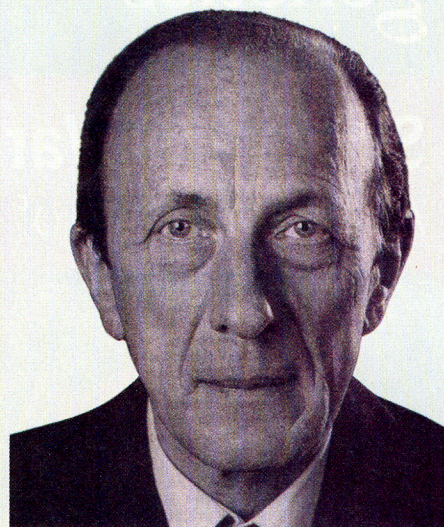
scope of research ranged from light absorption and energy transfer to the production of redox equivalents and the synthesis of ATP, the general-purpose fuel of life. His daring ideas, and above all his extraordinary perseverance, attracted a stream of ambitious and able young scientists to work under him.

During the ensuing years, this team of investigators marked off milestones in photosynthesis research. They found that excess light energy is disposed of harmlessly as heat through protective carotenoids. They discovered that the reactive pigment of photosystem II is chlorophyll *a*: its cationic form extracts electrons from the active site of water oxidation, with kinetics that depends on the electrostatics of charge accumulation. And they identified plastoquinone as an electron acceptor in photosystem II, where it functions as a one-to-two electron gate and as a mobile carrier between the two photosystems.

A further success was the use of electrochromic absorption transients from intrinsic photosynthetic pigments. These behave as ultra-rapid 'molecular voltmeters' to show that the primary electron-transfer reactions in both photosystems generate transmembrane voltage, and are thus directed across the photosynthetic coupling membrane. These vectorial reactions, together with associated proton uptake and release at opposite sides of the membrane, as hypothesized earlier by Peter Mitchell, were shown to generate the proton-motive force required for the synthesis of ATP.

But it was the mechanism of water oxidation that remained Witt's career-long preoccupation, his *spröde Geliebte* (prudish beloved). The manganese cluster in photosystem II is charged up with four oxidizing equivalents before it reacts with two water molecules, releasing dioxygen. Witt and his co-workers contributed valuable information on many aspects of the mechanism, including the valence changes of manganese, associated electrostatic changes and effects of extrinsic reductants. Despite these and other contributions from many laboratories around the world, understanding the detailed mechanism has remained a major challenge.

Witt's early attempts to crystallize photosystem II were fruitless, and it seemed that the game would be lost to others. However, crystals of photosystem I proved to be an initial consolation. With colleagues, including his wife Ingrid, Witt fine-tuned the crystallization procedure, and in 1993 produced crystals of photosystem I diffracting to 6 Å. The resolution was gradually improved



to 2.5 Å, revealing a beautiful trimeric structure with multiple subunits, diverse electron-transfer cofactors, about 100 chlorophyll molecules and many carotenoids, all in three-dimensional glory.

In 2001, together with a team led by Wolfram Saenger, also working in Berlin, Witt and his colleagues finally succeeded in crystallizing and analysing photosystem II, with a resolution of 3.8 Å. This structure was followed by the first refined model from James Barber's group, and then by the Berlin groups' further model based on slightly higher resolution. A full understanding of how photosystem II works remains one of the greatest challenges in biology.

Witt received numerous awards and honours, and more than 200 publications carry his name. His co-workers and former students, many of whom remained hooked on photosynthesis research, were fascinated by his seemingly permanent youth. Indeed, instead of growing into a father to his scientific offspring, he remained the ambitious elder brother — with its mix of fraught fraternal relations from time to time, but with spark, fun and high productivity when it came to science.

To those outside the inner circle, Horst Witt was a legendary figure from the early days of photosynthesis research. He had a tendency to divide members of the field into those of whom he approved (with whom he was open and charming, and relished robust argument) and those he did not: he could be intimidating. He was nevertheless universally respected for his sharp intellect and single-minded drive. Witt, who died on 14 May, leaves an unmatched legacy for those many scientists grappling with the intricacies of photosynthesis.

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