Photosynthesis Research
https://doi.org/10.1007/s11120-024-01102-9

HISTORY AND BIOGRAPHY

Remembering Jan Amesz (1934–2001): a great gentleman, a major discoverer, and an internationally renowned biophysicist of both oxygenic and anoxygenic photosynthesis[a]

Govindjee Govindjee[1] · Bas Amesz[2] · Győző Garab[3,4] · Alexandrina Stirbet[5]

Received: 8 February 2024 / Accepted: 18 April 2024

Abstract
We present here the research contributions of Jan Amesz (1934–2001) on deciphering the details of the early physico-chemical steps in oxygenic photosynthesis in plants, algae and cyanobacteria, as well as in anoxygenic photosynthesis in purple, green, and heliobacteria. His research included light absorption and the mechanism of excitation energy transfer, primary photochemistry, and electron transfer steps until the reduction of pyridine nucleotides. Among his many discoveries, we emphasize his 1961 proof, with L. N. M. Duysens, of the "series scheme" of oxygenic photosynthesis, through antagonistic effects of Light I and II on the redox state of cytochrome *f*. Further, we highlight the following research on oxygenic photosynthesis: the experimental direct proof that plastoquinone and plastocyanin function at their respective places in the Z-scheme. In addition, Amesz's major contributions were in unraveling the mechanism of excitation energy transfer and electron transport steps in anoxygenic photosynthetic bacteria (purple, green and heliobacteria). Before we present his research, focusing on his key discoveries, we provide a glimpse of his personal life. We end this Tribute with reminiscences from three of his former doctoral students (Sigi Neerken; Hjalmar Pernentier, and Frank Kleinherenbrink) and from several scientists (Suleyman Allakhverdiev; Robert Blankenship; Richard Cogdell) including two of the authors (G. Garab and A. Stirbet) of this Tribute.

Keywords Anoxygenic photosynthesis · Bacteriochlorophyll · Carnegie Institute of Washington · Cytochrome *f* · Chlorophyll · *Chromatium* sp. · Louis (Lou) N.M. Duysens · Electron transfer · Excitation energy transfer · Heliobacteria · Primary photochemistry · Reaction center · *Rhodopseudomonas* sp. · *Rhodospirillum* sp · Plastocyanin · Plastoquinone · Two-electron gate · Winkler Prins prize · Z-scheme

Introduction: personal, academic, and awards

We begin this *In Memoriam* by first giving a personal and then an academic background of Jan Amesz (1934–2001), a great biophysicist of our time. At the outset, we refer the readers to Jan Amesz's obituary (Hoff and Aartsma 2001, 2002) and to a special issue of this journal in his honor (Miller et al. 2002).

Personal

Jan Amesz was born in 1934 in Gouda, The Netherlands. His mother was Neeltje (Swanenburg) and his father Cornelis Amesz; they were married in 1931. Neeltje (born in 1907) was a housewife as was usual for a married woman at that time. Cornelis (born in 1903) worked as a

✉ Govindjee Govindjee
gov@illinois.edu

1 Department of Plant Biology, Department of Biochemistry, and the Center of Biophysics & Quantitative Biology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

2 Albertus Perkstraat 35, 1217 NL Hilversum, The Netherlands

3 Biological Research Centre, Institute of Plant Biology, HUN-REN, 6726 Szeged, Hungary

4 Department of Physics, Faculty of Science, University of Ostrava, 71000 Ostrava, Czech Republic

5 Anne Burras Lane, Newport News, VA 23606, USA

Published online: 30 April 2024

representative of *Goedewaagen Aardewerkfabrieken* (manufacturer of ceramic products, including pipes for smoking tobacco), located in Gouda. After 1960, Cornelis was self-employed selling pipes in the Netherlands. Jan would sometimes accompany him while he visited his clients.

Both of Jan's parents did not have the opportunity to continue their own education after primary school. This was felt as a loss and became an important motivation for them to seek every opportunity to support their four sons (Jan, Ad, Hans and Kees) for their studies. Since the family finances were insufficient to facilitate Jan's studies, a shop was opened, in 1951, opposite the Rijks HBS ("*Hogere Burgerschool*" for secondary school) in Gouda to sell chocolates, cakes and sweets; Jan's mother worked behind the counter six days a week to help the customers and the students. The income from this shop provided funds for Jan's education, and of his siblings.

In 1960, Jan Amesz was married to Anna Cornelia Uyttenbroek ('Ank'); they have three children: a daughter Stella; and two sons Robert and Bas. Further, Ank worked as a secretary at Leiden University (in the Department of Cultural Anthropology) and both Ank and Jan would always commute to the university together, as the Huygens Laboratory where Jan worked was close by to her office. The eldest son, Robert, became a software engineer, Stella became a specialist in treating complex wounds and Bas, the youngest, became a partner at a strategy consulting firm. Figure 1 shows the family of Jan at the home of Ank's parents in Oostvoorne, The Netherlands.

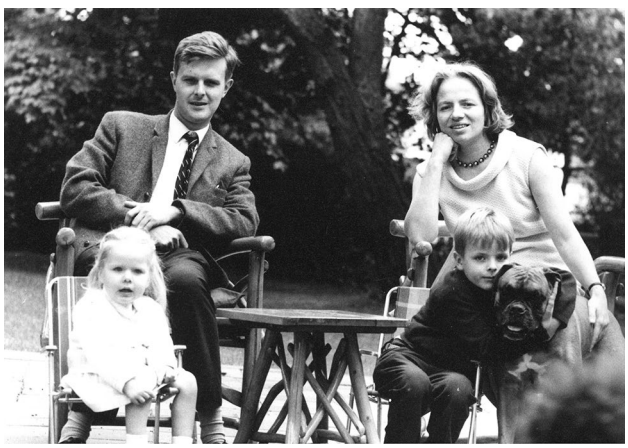

Fig. 1 A 1967 photograph of Jan Amesz and his family in the Netherlands—after their return from their trip to the Carnegie Institute of Washington, in Stanford, California. Top left: Jan Amesz; top right: Ank Amesz; bottom left: daughter Stella; bottom right: son Robert, with the family dog. The youngest (Bas) was not born yet. Source: Archives of the Amesz family

Academic

From his childhood, Jan was interested not only in science, but also in Arts and Literature. After graduating from the High School (*Gymnasium*) in Gouda, in 1951, he entered the Utrecht University (The Netherlands) where he studied Chemistry and obtained, in 1958, his Master's degree with honors.

Jan's work experience included his service as a '*Science Assistant'* at the University of Leiden (1958–1960) while he was a graduate student in Biophysics under the mentorship of Professor Louis (Lou) N.M. Duysens (for Duysens, see Govindjee and Pulles 2016). Then, in 1960, he was appointed as an *Assistant Professor* before he had obtained his doctorate. It was in 1964 that Jan obtained his Doctor of Philosophy, in Biophysics, with honors, from the University of Leiden, The Netherlands. In 1967, he was promoted to be an *Associate Professor*, and in 1979 to be a full *Professor* until 1999, extended as Emeritus till 2001, when he sadly passed away. (We note that Jan also served as the Chairman of the Department of Biophysics for several years in the 1980s.)

After his formal retirement in 1999, Jan cut down his administrative duties almost completely, but, scientifically, he remained fully active, especially with his last two graduate students (Hjalmar Permentier and Sigi Neerken; see their *Reminiscences*). Jan kept intensive contacts with them, planning experiments and discussing the results on a daily basis. He also had more time to sit with the students of the department at lunch or at coffee time and challenge them with all sorts of questions. With his sharp mind and a great sense of humor, Jan usually got the better of them in heated discussions that he clearly enjoyed! Evident from his high spirit and enthusiasm, his last years were very happy since he could devote his full attention to his great passion, which was science (see Hoff and Aartsma 2002).

Memberships and awards

Jan Amesz has been known to the scientific community as one of the topmost internationally renowned biophysicists related to both oxygenic and anoxygenic photosynthesis. He was a member of several professional societies including the Royal Netherlands Academy of Arts and Sciences, the European Society of Photobiology, the Netherlands Society of Biochemistry, and the Netherlands Society of Biophysics.

Most importantly, Jan Amesz was the 1970 recipient of the highly prestigious Winkler Prins prize of the Winkler Prins Foundation, for his outstanding research in unraveling the biophysical mechanism of photosynthesis, during

Fig. 2 Jan Amesz at the Winkler Prins prize ceremony in 1970, during the 100th anniversary of the Winkler Prins Encyclopedia in the Concertgebouw, in Amsterdam. From right to left: Prof. J.A. Ankum; Prof. J.A. de Jonge; Princess Beatrix; Jan Amesz; Ank Amesz (partially hidden); and the other two are Mrs. Ankum and Mrs. De Jonge (not sure of the order). Photograph by Bert Verhoeff. Source: Archives of the Amesz family

his doctoral research, and beyond. [Note that this prize is intended to promote scientific practice in the Netherlands and in Belgium.] Fig. 2 shows Jan Amesz at the reception of the Award Ceremony.

Below, we present an exposé of Jan Amesz's main discoveries, first with his mentor Professor Lou Duysens, and then with his own graduate students, postdoctoral associates, and colleagues in photochemistry, photophysics, biochemistry, and biophysics of photosynthesis in both anoxygenic and oxygenic photosynthetic organisms.

Research contributions of Jan Amesz

Jan Amesz has made extensive key contributions to the intricate details of the "light reactions" in both oxygenic and anoxygenic photosynthetic organisms—from the time light is absorbed to the time pyridine nucleotides are reduced. Figures 3 and 4, respectively, show the overall electron transfer schemes in key photosynthetic systems, and the arrangement of the pigment-protein complexes

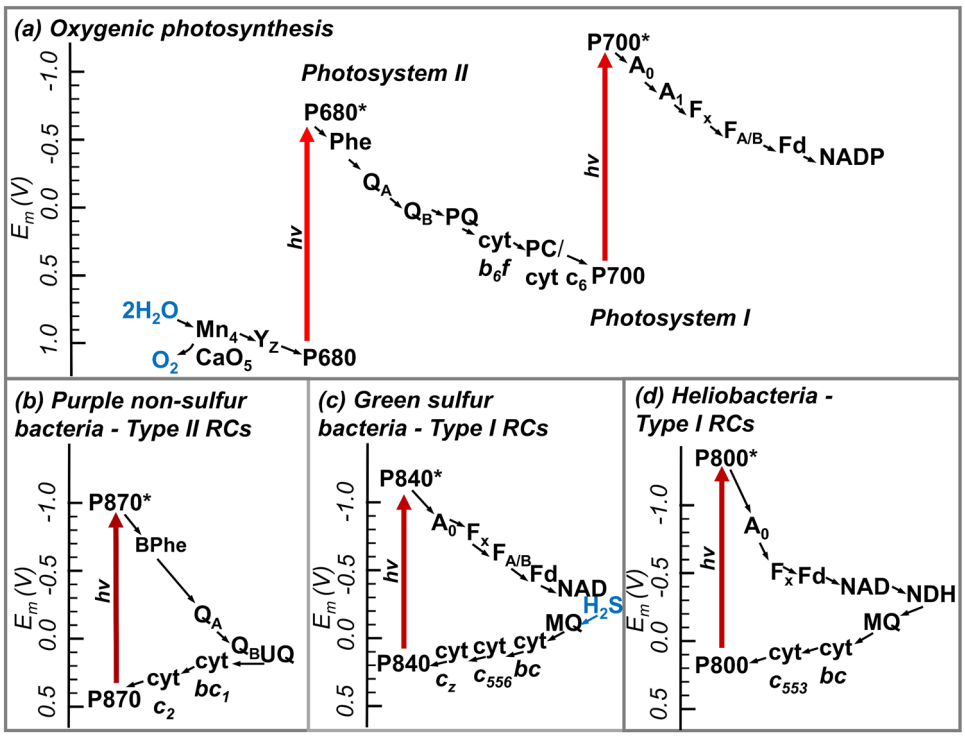

Fig. 3 Electron transport pathways in different photosynthetic organisms, with their electron carriers arranged according to their redox potentials. **a**: Oxygenic photosynthesis in plants, algae, and cyanobacteria, with two photosystems, PS I and PS II; **b**: Purple non-sulfur bacteria (e.g., *Rhodobacter sphaeroides*, which have Type II RCs (with pheophytin & quinone as electron acceptors); **c**: Green sulfur bacteria (e.g., *Chlorobaculum tepidum*), which have *Type I RCs*; they use iron-sulfur reaction centers as electron acceptorsand **d**: Heliobacteria (e.g., *Heliobacterium modesticaldum*), which also use *Type I RCs*. For further information on both oxygenic and anoxygenic photosynthesis, see Blankenship (2021), on c-type cytochromes in the photosynthetic electron transfer of anoxygenic photosynthetic bacteria, see Azai et al. (2010), and for the electron transport in the RCs of all photosynthetic organisms, see Kanda and Ishikita (2023)

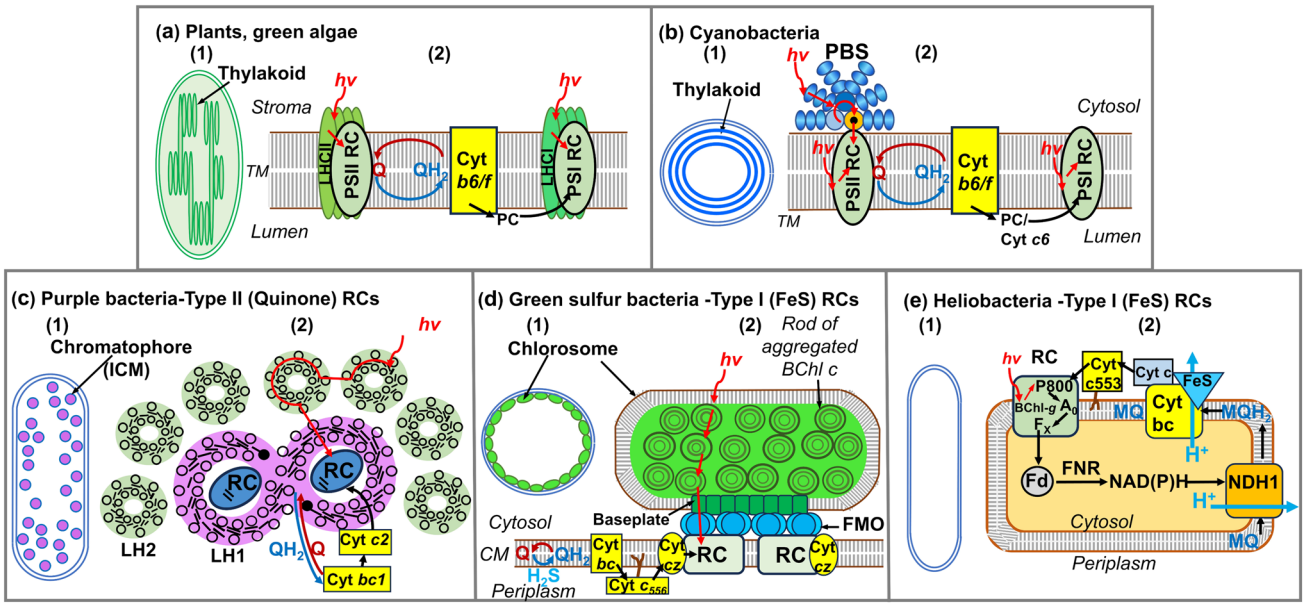

Fig. 4 Schematic representation of light harvesting apparatus and photosynthetic electron transfer in different photosynthetic organisms. **a** Plants and green algae: (1) A chloroplast with its thylakoid membrane system; (2) Photosystem I (PSI) and Photosystem II (PSII), with their light harvesting antenna complexes (LHCI and LHCII), in the thylakoid membrane (TM), as well as the electron transport system including PSII, PSI, the cytochrome (Cyt) b_6f complex, and the mobile electron carriers plastoquinone (Q) and plastocyanin (PC). **b** Cyanobacteria: (1) A cyanobacterial cell with its thylakoid membranes; (2) PSI and PSII cores in the TM, with phycobilisomes (PBS—containing phycobiliproteins and linker proteins) as mobile antenna (that can move from PSII to PSI and vice versa), as well as the electron transport from PSII to PSI via the Cyt b_6f complex, and the mobile electron carrier plastoquinone (Q), and PC or Cyt c_6. **c** Purple bacteria, e.g., *Rhodobacter sphaeroides*: (1) A purple bacterial cell with its intracytoplasmic membrane system (IMS), consisting of vesicular chromatophores of 50–70 nm diameter; (2) dimeric RC (reaction center)–LH1 protein complex surrounded by several units of accessory LH2 complex, in the chromatophore membrane, as well as the cyclic electron transport via the Cyt bc_1 complex and the mobile electron carriers ubiquinone (Q) and Cyt c_2. **d** Green sulfur bacteria, e.g., *Chlorobaculum tepidum*: (1) A green sulfur bacterial cell with chlorosomes attached to the cytoplasmic side of the plasma membrane; (2) A chlorosome containing accessory light harvesting pigments, which self-aggregate in the form of a multiwall helical arrangement of syn-anti stacked bacteriochlorophyll (BChl) molecules in cylinders (rods) and/or in spirals of ~ 10 nm diameter; light energy captured in these rods is transferred to the RCs in the cytoplasmic membrane through BChl *a* molecules in the baseplate proteins, via the Fenna-Matthews-Olson (FMO) protein units. The cyt c_Z subunit in the RC complex mediates electron transfer to the BChl pair P840 in the RC, mainly from menaquinol (Q)/cytochrome oxidase (Cyt *bc*), with the membrane-anchored Cyt c_{556} functioning as a shuttle-like electron carrier between Cyt *bc* and Cyt c_Z. **e** Heliobacteria, e.g., *Heliobacterium modesticaldum*: (1) A heliobacteria cell, in which the light harvesting pigments (i.e., 54 BChl *g* molecules) are part of the internal antenna of the RCs, which are located in the plasma membrane; (2) The excitation energy harvested by the internal antenna is transferred to the primary electron donor, P800, which is a special BChl *g′* pair. After the transfer of an electron from P800* to the primary electron acceptor A_0, the electron is transferred to F_X (a Fe-S cluster). From the reduced F_X the electron is transferred to the menaquinone (MQ) pool via ferredoxin (Fd), ferredoxin:NADP$^+$ oxidoreductase (FNR), the NAD(P)H pool, and a proton-translocating NAD(P)H:quinone oxidoreductase (NDH-1). This is then followed by the oxidation of MQH_2 and the reduction of the membrane attached Cyt *c553* via the Cyt *bc* complex, also coupled with proton pumping, after which, Cyt *c553* finally reduces the P800$^+$. The protons released are used to synthetize ATP. For information on both oxygenic and anoxygenic photosynthesis, see Blankenship (2021), and for the c-type cytochromes in the photosynthetic electron transfer of anoxygenic photosynthetic bacteria, see Azai et al. (2010)

involved in the excitation energy transfer and other reactions in the various systems. We shall refer to these figures (for details, see their legends), which reflect our present understanding of these processes, to illustrate the significance of selected discoveries of Jan Amesz—during 1957–1969; 1970–1985; and 1986–2001.

The 1957–1969 period

These years in photosynthesis research could perhaps be characterized best by discoveries of basic processes of the 'light reactions', in which Jan Amesz, as a PhD student and young scientist, made very important contributions.

Quantum yield of NAD and NADP reduction

Jan Amesz began his research career in 1957 in the Biophysics Laboratory of Louis (Lou) Duysens. His first paper (Duysens and Amesz 1957) included experiments on developing a sensitive fluorescence method to monitor the formation of reduced nicotinamide adenine dinucleotides (NADH and NADPH) in photosynthetic systems (Figs. 3a and 4a). Jan's method was a wonderful way to, measure quantum yield of NADP reduction—and this is what was done by him (Duysens and Amesz 1959); it was just right to match with the known ~ 12 minimum quanta for the evolution of one O_2 molecule.

Key contributions on Z-scheme intermediates

Jan Amesz, working in Lou Duysens's Lab, discovered in the red alga *Porphyridium cruentum* that "Light 1" (red light, absorbed by chlorophyll a) oxidized cytochrome *f* (Cyt *f*) and "Light 2" (orange light, absorbed by phycoerythrin) reduced the oxidized Cyt *f* (Duysens et al. 1961) (see Figs. 3a and 4a). This antagonistic effect of Light 1 and Light 2 is key to the acceptance of the "Z" scheme of oxygenic photosynthesis. Further, Duysens and Amesz (1962) showed that (i) the herbicide diuron [DCMU; 3-(3,4-dichlorophenyl)-l,l-dimethylurea] blocks the reduction of Cyt *f*, but not its oxidation; and that (ii) both the Pigment Systems (PSI and PSII) contain chlorophyll *a* (Chl *a*) as well as accessory pigments, but PSI contains more of Chl *a* than the accessory pigments, whereas PSII has the reverse in agreement with the concept of others (see a review by Govindjee (2023); and Figs. 3a and 4a). Further, Amesz and Duysens (1962; also see Duysens and Amesz 1962) extended the above observations to cyanobacteria: Cyt *f* in the middle and NADP at the end of the electron transport chain. These were remarkable discoveries of Jan Amesz (also see Amesz 1964a, b and Amesz et al. 1971).

Further, Amesz and Fork (1967)—during the postdoctoral fellowship of Jan Amesz at the Carnegie Institution of Washington at Stanford, California—obtained key quantitative information on the functioning of both P700 (reaction center of PSI) and Cyt *f* in the red algae *Iridaea splendens* and *Schizymenia pacifica* by showing that the efficiency of redox changes of these components was very high. Figure 5 shows a group photograph when Jan was at the Carnegie Institute. It was also about that time that Duysens and Amesz (1967) provided a full discussion of the entire "Light Reaction" part of "Photosynthesis".

Fig. 5 A late 1960s group photograph at the Carnegie Institute of Washington (CIW), Stanford, California. On the top (1st on the left) is Janet S. Brown, whereas David C. Fork is 3rd from the left (sitting on the steps in the back row); on his right is William M. Hiesey, and on his left bottom is Director C. Stacey French. Jan Anderson is 3rd from the right in the top row, and on her left is Jan Amesz (with his right hand touching his head), and on his left is Malcolm A. Nobs. Source: Plant Biology, CIW

What anoxygenic photosynthetic bacteria do: one light reaction, or two?

Based on the observations of similar action spectra for bacteriochlorophyll fluorescence, and more, Amesz (1963) had concluded that *only one pigment system is present in purple bacteria* as opposed to cyanobacteria, algae, and plants (cf. Figure 3b with a; also see Fig. 4). Further, when Vredenberg et al. (1965) reexamined absorbance changes both in BChl *a* and carotenoids in several purple bacteria, they concluded that these changes were due to electrochromic shift due to the electric field generated across the membrane (also see: Amesz and Vredenberg 1966). In addition, Vredenberg and Amesz (1966) made an important conclusion that some of these absorbance changes were due to conformational changes during photosynthesis.

The 1970–1985 period

In this one and a half decade, Jan Amesz established himself as an internationally renowned biophysicist in the field of photosynthesis research. His research contributed significantly to all what we know about the molecular organization of the photosynthetic membranes in anoxygenic and oxygenic organisms (Fig. 4) and the electron transfer processes (Fig. 3); for details, see the figure legends.

Anoxygenic photosynthetic bacteria

Jan Amesz published pioneering research on the composition, the arrangement, and the function of the

light-harvesting pigments, as well as the photochemistry and the structure of photosynthetic reaction centers (RCs) of anaerobic purple non-sulfur bacteria, green sulfur bacteria and heliobacteria.

Using RC preparations from the purple bacterium *Rhodopseudomonas* (*R.*) *sphaeroides*, Romijn and Amesz (1976) showed highly efficient ubiquinone reduction at 100 K—clearly establishing the role of quinones in primary photochemistry (see Figs. 3b and 4c). In addition, they revealed that the reduction of ubiquinone was accompanied by a shift of the infrared absorption band of bacteriopheophytin, and provided detailed information on the temperature dependence of both the forward and the reverse reactions of the primary events in *R. sphaeroides*. Then, De Grooth and Amesz (1977) published quantitative information on light-induced absorption changes due to the photo-oxidation of the reaction center (P870) in the chromatophores of *R. sphaeroides*, and concluded that P870 is located inside the membrane (see Fig. 4c). Besides the membrane potential due to the electron transfer from P870 to a primary electron acceptor, they observed the generation of an additional membrane potential due to the electron transfer from a Cyt *c* to $P870^{+}$. These observations were followed by Rijgersberg et al. (1979, 1980) publishing thorough investigations on the absorption and emission spectra of several purple bacteria as a function of temperature down to 4 K and identifying an absorption band at 751–757 nm to be due to bacteriopheophytin in the RC!

Swarthoff and Amesz (1979) investigated photochemical activities of BChl *a*-protein complexes from the green photosynthetic bacterium *Prosthecochloris* (*P.*) *aestuarii*, which was shown to contain 35–75 BChl *a* molecules per RC. Fluorescence properties of these cells and their subcellular preparations were explored by Karapetyan et al. (1980). Then, Swarthoff et al. (1981) discovered that the absorption decrease at 836 nm was due to the oxidation of the RC P840, which was accompanied, at 80 K, by band shifts of antenna BChls at 797, 816 and 833 nm. In addition, a detailed picture of the excitation energy transfer from the antenna to the RC and photochemistry, as a function of temperature, was presented, ending with a clear and thorough summary of all the primary events in this green bacterium. This was followed by Swarthoff et al. (1982) providing detailed information on the pigments of photochemically active protein complexes, and showing that these complexes did not have BChl *c*, which is,however, in high quantity in intact cells. Kramer and Amesz (1982) presented data on the effects of magnetic field on the light emission from the complexes mentioned above, which suggested that a part of the observed light emission is delayed fluorescence (or delayed light emission, DLE), which is due to the reversal of the primary reactions at the RCs. Vasmel et al. (1983), studying the RC of the green bacterium *Chloroflexus aurantiacus*, concluded that the primary electron donor is a BChl *a* dimer, as is also the case in purple bacteria. It was Nuijs et al. (1985a), who carrying out picosecond absorbance difference spectroscopy, arrived to the (at that time, tentative) conclusion that in the green bacterium, *P. aestuarii* the secondary acceptor molecule is an iron-sulfur center.

In the mid 1980s, Jan Amesz's group included in their research the newly discovered photosynthetic bacterium *Heliobacterium* (*H.*) *chlorum*. Nuijs et al. (1985b) in their seminal work, using the most up-to-date ultrafast spectroscopy techniques, concluded that the primary photochemistry of *H. chlorum* is very similar to that of green sulfur bacteria (see Figs. 3d and 4e). A more detailed characterization of these processes, and of the organization of the antenna, as well as the energy transfer events prior to the actual photochemical charge transfer were given by van Dorssen et al. (1985).

Oxygenic photosynthesis

Perhaps the most important discovery of Jan Amesz in this period of time was the existence of two-electron gate at the electron acceptor side of PSII, a "hypothetical electron carrier situated between Q [now Q_A] and plastoquinone" (Amesz 1973; Velthuys and Amesz 1974). This conclusion was reached by measuring an increase of Chl *a* fluorescence induced in darkness by adding, e.g., DCMU to chloroplasts where the system was set up to get electrons from an artificial electron donor rather than water, and via observing that there was a unique flash-number dependence in Chl *a* fluorescence: it was larger after odd (1 and 3) than after even flash numbers (2 and 4). Interestingly, the concept of two-electron gate was also suggested by Bouges-Bocquet (1973) via the detection of Period 2 oscillation of electrons on the acceptor side of PSI, arriving from PSII.

Amesz and coworkers made a range of other important discoveries using Chl *a* fluorescence measurements. Kraan et al. (1970) concluded that the observed increased DLE was due to increased back reaction of the primary photoproducts of PSII. Further, they presented data on salt-induced DLE, indicating that there must exist a diffusion potential across the thylakoid membrane: positive on the inside with respect to the outside of the thylakoid membrane. In addition, Jan Amesz and his coworkers recognized the importance of the integrity of the thylakoid membrane in their research, with the reduced primary acceptor of PSII on the outside and the oxidized primary donor on the inside, leading to DLE occurring by the back reaction in a pH-dependent manner. Amesz and van Gorkom (1978) summarized, in a thorough manner, the literature on DLE as well as thermoluminescence in photosynthetic systems (see also Amesz and de Grooth 1976). Rijgersberg et al. (1979), based

on fluorescence spectroscopy of PSI and PSII complexes, as well as of Chl *b*-less mutant between 100 and 4 K, concluded that the emission at 680 nm is from [LHCII] and the bands at 685 and 695 nm are from PSII pigment-protein complexes.

An important result was obtained in Amesz' Lab also on the different components of the intersystem and PSI electron transport system (see Figs. 3a and 4a) and on the energization of thylakoid membranes. Amesz et al. (1972) showed that cytochrome *b* does not form a part of the linear chain of electron flow; this was in contrast to what was proposed in the Hill and Bendall (1960) scheme. Further, Amesz and coworkers determined the pool sizes of Cyt *f* and plastoquinone relative to P700 to be 2 and 15 electron equivalents, respectively. Later, Visser et al. (1974) focused on plastocyanin (PC), using EPR spectroscopy at 20 K and pointed out that this copper-containing protein acts between the two photosystems and that it is also involved in the PSI cyclic electron transfer pathway. Amesz and Visser (1971), using many different algae, observed absorption changes in the 640–710 nm region; these absorption changes, along with those around 518 nm ('P518'), were later identified as electrochromic absorption transients (Amesz and de Grooth 1976).

The 1986–2001 period

During this period, Jan Amesz, as one of the leading scientists in the biophysics of photosynthesis worldwide, focused on uncovering important details in the primary processes in anoxygenic photosynthetic organisms—with most important contributions on the green bacteria and the heliobacteria. As a distinguished professor, he continued his invaluable service to our community by educating—directly or indirectly—generations of 'photosynthetikers', as the late Jack Myers may have said.

Anoxygenic photosynthetic bacteria

Nuijs et al. (1986), studying picosecond to nanosecond processes in the antenna as well as in the RCs of the green bacteria *Chloroflexus aurantiacus*, provided detailed information on all the steps from the time light was absorbed to the time electrons reached the secondary electron acceptor. Shuvalov et al. (1986), using *P. aestuarii*, showed that the primary charge separation takes place within 10 ps. Exploration of the mechanisms of light harvesting and photochemistry, in both green bacteria and heliobacteria, went hand-in-hand during 1986–2001 in Amesz' Lab (cf. Figs. 3c,d and 4d,e).

Van Dorssen et al. (1986a) studied the primary photochemical events in chlorosomes of the green bacterium *Chl. limicola* and showed that BChl *a* is responsible for transferring excitation energy to where the rest of the machinery is located. Van Dorssen et al. (1986b), by exploiting measurements on fluorescence polarization and linear dichroism, mapped the orientation of pigment dipoles—this information became highly useful in understanding the details of the overall excitation energy process in this organism. Van Grondelle and Amesz (1986) have summarized the entire process of excitation energy transfer in a highly thorough review. Two years later, van Dorssen and Amesz (1988) concluded that BChl *a* is associated with the baseplate of the chlorosome (see Fig. 4d). Vos et al. (1987) concluded from ultrafast transient absorption spectroscopy data that a chlorosome serves as a common antenna for several reaction centers. It was Otte et al. (1991) who emphasized the similarity in the structures of the main light harvesting pigment in three different photosynthetic bacteria: *P. aestuarii* that has BChl *c*, *Chl. vibrioforme* that has BChl *d*, and *Chl. phaeovibrioides* that has BChl *e*. Steensgaard et al. (2000) described excitation energy transfer processes in *Chl. limicola* chlorosomes, which has 50% BChl *c* and 50% BChl *d*.

In most of his work, Jan Amesz had not really focused on the so-called "Fenna-Matthews-Olson" (for short FMO) protein, which is located between the baseplate and the cytoplasmic membrane and is key to the transfer of excitation energy from the chlorosome to the RC (see Fig. 4d). However, in Francke et al. (1996), Amesz joined John M. Olson to examine (by absorption and fluorescence spectroscopy at 6 K) the FMO protein from *Chlorobaculum* (*Chl.*) *tepidum* −and determined the energy transfer efficiencies. Francke and Amesz (1997) developed new and quick methods to isolate pure and clean preparations of chlorosomes and the FMO-proteins from different bacteria. We note that Vulto et al. (1998, 1999a) had dug still deeper into the structure and the dynamics of the FMO complex from both *P. aestuarii* and *Chl. tepidum*; they also compared the excited state dynamics of the FMO complex and the experimental data for its function in both *Chl. tepidum* and *P. aestuarii,* as obtained from pump-probe measurements at cryogenic temperatures.

Van de Meent et al. (1991, 1992) examined various species of green sulfur bacteria and showed what is common between the various RCs: the primary electron acceptor, an isomer of Chl *a* (see A_0 in Fig. 3c), emphasizing a commonality between the reaction centers of green sulfur bacteria, heliobacteria and PS I (for heliobacteria, see below).

Using pump-probe transient absorption spectroscopy, Neerken et al. (1998; also see Neerken's *Reminiscences*) provided detailed information on the very primary photochemical events, not only in the RC core complex of *P. aestuarii* and its FMO complex, but also in the two together. For example, Sigi Neerken and her coauthors observed that the excitation energy transfer from Chl *a* 670 to BChl *a* takes

Fig. 6 Jan Amesz playing table tennis with Lou Duysens. This was in the hallway, outside the Biophysics Laboratory, at the University of Leiden**.** What is interesting is that Jan is wearing a tie and playing with his former thesis professor, but then a colleague. Date and photographer unknown. Source: Archives of the Amesz family

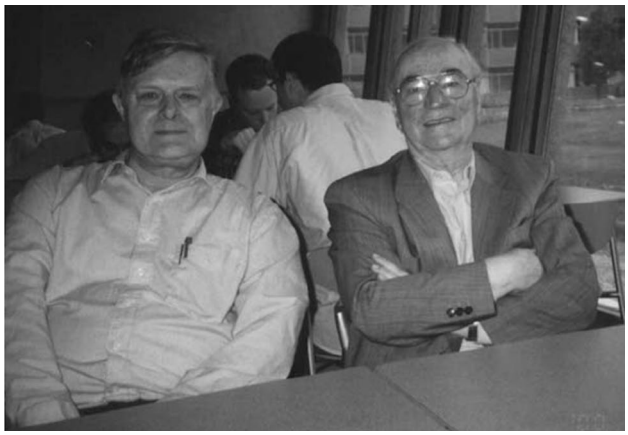

Fig. 7 Jan Amesz (left) and Lou Duysens (right) at the time of Duysens' retirement in 2000. Photograph was provided by the late Howard Gest

place within 1.2 ps, the latter decaying in 25 ps, which is due to trapping of the energy in the RC complex. Then, Neerken et al. (2000a) provided a detailed and thorough picture of the primary events in *Heliobacillus mobilis* at 10 K as well as at 275 K, by using sub-ps difference absorption spectroscopy. Permentier et al. (2000a, b; see *Reminiscences* by Permentier) provided a detailed and thorough analysis of the composition and the primary function of the RC complexes of two green sulfur bacteria, *P. aestuarii* and *Chl. tepidum*.

During the period Jan Amesz was on the faculty at Leiden and Lou Duysens was still the head of Biophysics, Jan would take time off to play table tennis; Fig. 6 shows Jan playing with Lou Duysens.

Going back to research, Smit et al. (1987) established that, in the brownish green bacterium *H. chlorum* (see Figs. 3d and 4e), the primary electron donor is P798 (P800); van Kan et al. (1989) revealed that the primary electron acceptor (i.e., A_0 in Figs. 3d and 4e) is a Chl *a* -like pigment with an absorption band at 670 nm. A year later, van de Meent et al. (1990) reported that the spectral properties of the isolated antenna-reaction center complexes are similar in *H. chlorum* and *Heliobaccilus mobilis*. We note that the existence (and possible functioning) of BChl *g*' in *H. chlorum* was *unequivocally* demonstrated by Kobayashi et al. (1991); then, an important conclusion was made by Van de Meent et al. (1991) who clearly established, by HPLC, NMR as well as by optical and mass spectroscopy, that the primary electron acceptor of all heliobacteria is *8*^{1}*-hydroxychlorophyll a.* Soon thereafter, van Noort et al. (1992) provided key information on the energy transfer and primary photochemistry in *H. chlorum* and concluded that the primary charge separation must be an extremely rapid process.

The paper by Neerken and Amesz (2001) is the very last one that Jan Amesz has published—it is basically his 'final' view on the photosynthesis of heliobacteria, as known since 1995. It deals with the organization of the antenna and focusses on the pigments there: BChl *g*, the main pigment, a very special Chl *a*, which is the primary electron acceptor here (see above), as well as a special carotenoid with more than two dozen carbon atoms. Within just a few ps, the antenna (~ three dozen BChls *g*) completely equilibrate the absorbed photons. Then, there is the charge separation, where P798 (a BChl *g'* dimer) is the primary electron donor and a special hydroxy Chl *a* is the primary electron acceptor (i.e., A_0).

Figure 7 shows a photograph of this time period, of Jan Amesz with Lou Duysens, at Leiden University.

In Amesz' Lab advanced, top-notch spectroscopic techniques were also applied to explore the excitation energy and primary photochemical pathways in purple bacteria (cf. Figs. 3b and 4c). Here we provide only a brief description of this topic—noting that all results are at the highest level and have contributed much to our present understanding of these processes.

Vos et al. (1986) observed a strong temperature decrease in the rate of excitation energy transfer between the antenna molecules and a somewhat weaker one from the antenna to the RC—when the sample was cooled from room temperature to 4 K. Deinum et al. (1989) performed exciton annihilation studies from 300 down to 4 K. Then, Kleinherenbrink et al. (1993) compared purple bacteria with a heliobacterium—in collaboration with Robert Blankenship (of USA; see his

Reminiscences). Further, Otte et al. (1993) have shown that the efficiency of energy transfer from the RC to the antenna is very low—demonstrating that the rate of photochemistry is controlled by the rate of energy transfer from the antenna to the RC, as is the case in most other systems. By using difference absorption spectroscopy, and 200 fs excitation flashes, Kennis et al. (1996) discovered that energy transfer from BChl 800 to BChl 850 in purple bacteria occurs within 0.8–0.9 ps. Quite interestingly, Kramer and Amesz (1996) provided evidence for the existence of "uphill" excitation energy transfer from BChl 920 to BChl 800–850, see also Permentier et al. (2000b), who showed the same in a newly identified purple non-sulfur bacterium *Roseospirillum parvum* strain 9301. Kennis et al. (1997a, b) have provided us all the intricate details of the very early events in the primary photochemistry and photophysics of purple bacteria—from femtoseconds to picoseconds! Vulto et al. (1999b) examined the relaxation of excitation energy in the B850s of LH2 of *Rhodopseudomonas acidophila* at 7 K using two-color femtosecond absorption spectroscopy. Although much remains to be studied to get the final picture, the seminal research from Jan Amesz's Lab serves as the basis for elucidating the physical mechanism of exciton relaxation dynamics in LH2 (see e.g., Kim et al. 2022).

Reviews, edited books

It was during the mid 1980s that one of us (Govindjee) had the greatest (in-depth) association with Jan Amesz, when the two, together with David Fork, edited a book (Govindjee et al. 1986) that included everything that was known about light emission and their importance in understanding the physiology, biochemistry, and biophysics of photosynthesis. Authors, selected by this trio, were top international scientists. It was during this time period that Govindjee recalls what he thought was hilarious. When any author would not agree to accept the suggestions of any of the editors, Jan would say"If he wants to make a fool of himself, let him do that" whenever they would be pushing only their own views!

Amesz (1991) has provided a thorough review on all aspects of green photosynthetic bacteria as well as heliobacteria (see also Kobayashi et al. 1992). In a book, edited by Blankenship et al. (1995), Amesz (1995) provided a clear and succinct summary of all that was known about the photosynthesis of anoxygenic bacteria till 1994. Francke and Amesz (1995) have provided a clear summary of the field of the nature of BChl in green bacteria.

Earlier, Amesz (1987) had edited a book on the overall process of photosynthesis, and then published an excellent review of all aspects of "Biophysics of Photosynthesis" (Amesz 1989). Furthermore, Amesz and Hoff (1996) edited an important book on "Biophysical Techniques in Photosynthesis" in the Advances in Photosynthesis series. Here, all the chapters are clear and to the point and are still used in courses for M.Sc. and Ph.D. students. These are additional reasons for graduate students around the World to appreciate the contributions of Jan Amesz for their education. Duysens (1989), Jan's own PhD advisor, provided a perspective of his own research and that of his research group including that of Jan Amesz; it is a very important article for all who are interested in the 'anatomy' of important discoveries, emphasizing the importance of new powerful methods as well as of new theories.

It was in 1996 that Jan Amesz, together with Govindjee and Robert Knox honored William Arnold, the pioneer of most of the biophysical processes of photosynthesis (see the editorial in: Govindjee et al. 1996). For the evolution of the concept of the "reaction center" and the contributions of Lou Duysens, Jan Amesz's doctoral advisor, we recommend the paper by van Grondelle and van Gorkom (2014).

Reminiscences

From the family of Jan Amesz by Bas Amesz (e-mail: bamesz@vintura.com)

My brother Rob, sister Stella and I remember our father as a man of reason; rational thinking, logic and the pursuit of knowledge were in his DNA. In his early years, he was convinced that education would elevate mankind, bring well-being to all, and reduce conflict. He was married to our mother, Ank Amesz who was a secretary at Leiden University and they would drive to work together every day from our home which was in the town of *Leiderdorp*, near the city of Leiden.

Our parents held a modern, no-nonsense view when it came to bringing up their children. For example, as far back as we can remember we called them by their first names, which was quite uncommon at the time in the Netherlands.

Jan didn't care much for material things. He would proudly sport an inexpensive tie from a very basic textile shop, nor was he bothered about driving the latest model of a car—a simple second-hand one did the job just fine for him. The only thing he considered worth spending real money on was education and personal development, and in this, he was happy to support us in full. He was very supportive when it came to Stella's passion for horseback-riding, to the extent that he even bought her a horse when she wanted to pursue a career in it.

Jan, our father, was a man of routine. He would always fall asleep on the couch watching the eight o'clock news, only to wake up about an hour later to read the newspaper before finishing off the evening with some work.

My father was always eager to teach people things. He would tell stories of Greek mythology when driving Robert to swimming classes and take strolls through the

garden with his granddaughter, pointing out different plant species and insects. During my high school days, he was always there to support me in preparing for tests and exams. A pleasant surprise to many is that he was able to give lectures on any topic; for me, I enjoyed those on history the most. He would often say '*your textbook is explaining this incorrectly so learn this for your test, but know that in reality THIS is what really happened'*. In this, he taught me a valuable lesson that the truths often don't exist; they are rather perspectives to understand.

In the 1980s, Jan and Ank bought a tiny second house near the coast. It was their escape from everyday life, and they loved it so much they would spend nearly every weekend there. During our countless walks on the beach, preferably in the evening when it was nice and dark, we would talk about the week that had just passed. During these times, he would always point out the constellations, such as the '*Big Dipper'* or '*Cassiopeia*'. He was always fascinated by astronomy and sometimes even contemplated the idea of studying this at the university.

In his work, visiting countless conferences with his (international) colleagues and working with his Ph.D. students were the things that gave him the most pleasure and satisfaction. It was later in life that there was more room for emotional feelings rather than just reasons and logic. He stopped wearing a tie and became much more informal. He really enjoyed the period after his official retirement as a full Professor and the Department Head. With less stress on his shoulders, he could fully focus on his students, engage in stimulating discussions with colleagues and enjoy nice weekends with Ank in their summer home.

After Jan's passing away, we were fortunate to experience two of his students (Sigi Neerken and Hjalmar Permentier) defending their doctoral theses after Jan's death, which was very special. Our mother Ank had a hard time after Jan was no-more, but with time, she picked up life again in good spirits. A year and a half after Jan's death, Ank passed away peacefully in her sleep. After more than 20 years, we still miss them every day.

Sigi Neerken (e-mail: sigi.neerken@innosignbio.com)

About 25 years ago, I had the privilege of working with Jan Amesz as one of his last PhD students. I just had completed my master's degree project in the same biophysics group at Leiden University under the supervision of Thijs Aartsma, and was lucky to continue working in this vibrant environment.

As Jan's student, I got to know him as a dedicated professor, jointly leading the biophysics group alongside Arnold Hoff, Thijs Aartsma and Hans van Gorkom, with a substantial group of PhD students, postdocs and supporting staff, to advance the research in photosynthesis.

Jan was incredibly productive, and I witnessed one PhD student after another successfully completing their theses under his guidance. With his busy schedule, I remain impressed how Jan managed to be approachable and friendly. Whenever someone knocked on his door, despite being in the midst of something, he made time to respond in a friendly and a highly helpful manner.

Even when Jan was retiring from his formal duties in 1999, he enjoyed concentrating on the science and on mentoring a smaller group of PhD students and post-docs.

It was the time when femtosecond laser spectroscopy was emerging as a powerful tool to study energy conversion in photosynthetic plants and bacteria. My research was leveraged on the one hand, by the unique home-built amplified dye-laser system (built by John Kennis) with a time-resolution of 300 fs, which was able to capture a broad spectrum over 150 nm in one-go, and on the other hand by the recent isolation protocols for photosynthetic complexes (as developed by Christof Francke, Hjalmar Permentier and Arjo de Boer).

With these key advances, in his research group, Jan became highly interested in unraveling the steps involved in excitation energy transfer in various pigment-protein complexes of photosynthetic bacteria. While I was trying to keep the dye-laser operational for as long as possible, Jan could hardly wait to see the results of the measurements, and to begin interpreting, discussing, and proposing new ideas for future experiments. Frequently in the mornings, he would announce "my pen flowed" and he would pass long pages of handwritten text containing his findings and thoughts about the results of the previous days.

Possibly the most crucial lesson I learned from Jan Amesz, and I continue to apply almost daily, occasionally to the annoyance of my current colleagues, is the skill of writing. I recall my initial attempt at writing my first article, handing him a piece of my text, and getting, in return, pages of his handwritten revisions; only certain parts of my original sentences were cut out with a pair of scissors. While this was challenging to me at that time, I am (and have been) grateful for those lessons. I would like to add that most of Jan's PhD students felt (and feel) the same way as I did.

In his final years, Jan had more time to enjoy the interactions with his group. I have fond memories of our visit to the International Symposium on Phototrophic Prokaryotes in Barcelona in 2000, together with Hjalmar Permentier, Kristiane Schmidt and Frank Nowak. Beyond the scientific program we enjoyed the sightseeing in Park Güell. With his sharp mind and sense of humor, Jan enjoyed sharing his perspective on various topics, often

aiming to provoke a response. He always took pleasure to teach Dutch expressions, not only to the non-Dutch members of his team, but anyone interested.

In January 2001, right after my PhD thesis was completed and sent to the printer, Jan informed us about his upcoming surgery. It was a shock to us all when we learned about his sudden death due to complications arising from the surgery.

Certainly, Jan would have undoubtedly been proud to witness his last two PhD students completing their formal doctoral ceremony. (For references to our published research, see section II.C; and Reminiscences by H. Permentier). I have dedicated my thesis to Jan, grateful for the invaluable experience of his leadership, mentorship, and friendship, which truly enriched and shaped my life in ways I'll always treasure.

Hjalmar Permentier (e-mail: h.p.permentier@rug.nl)

As one of Jan Amesz's last PhD students, I first met him when I started my thesis project on photosynthetic bacteria in 1996 at the Biophysics Department of Leiden University. Initially, the plan was to work on Photosystem II of green algae, but Jan's main interest had shifted to purple and green sulfur bacteria, so these became my focus for the next 4 years, resulting in my doctoral thesis entitled "*Light-harvesting and core complexes of anoxygenic phototrophic bacteria*".

I was lucky to get a running start, as I could build upon the work of my predecessor, Christof Francke, who had recently devised a method to isolate the intact reaction centers of *Prosthecochloris aestuarii.* He gave me a crash course on the spectroscopy instrumentation in the Biophysics lab, but it was still a daunting environment for a student of biology like myself.

I have fond memories of my time in the Biophysics lab in Leiden, a great and dynamic group with Jan emerging as a kind of father figure in those days. To my surprise I heard that Jan had a bit of a reputation in the group because of his temper and impatience with certain people in the University. I got along great with him from the start, and I can only assume that Jan had grown milder during the years before his official retirement, because he could step away from the university politics and focus more on the science that he loved.

Our weekly research meetings, usually with Sigi Neerken, Kristiane Schmidt and Frank Nowak, were a highlight, where after critically reviewing everyone's research progress, current affairs and politics were discussed, triggered by the newspapers that Jan always brought. He took great pleasure in challenging our preconceptions and political beliefs. I believe that this also helped to sharpen our minds for scientific discussions. Writing clear and accurate scientific texts was another great skill that Jan taught us, correcting our attempts at manuscripts with extensive written changes in his typical hand. As a result of his help, my PhD period was a relatively smooth affair and with the frequent feedback of Jan, both Sigi and me were able to finish our theses in time. Together with Jan, as well with many others in his research group, we published several detailed papers on the primary events, especially excitation energy transfer in green bacteria (Neerken et al. 1998, 2000b; Permentier et al. 2000a; Schmidt et al. 2000; Steensgaard et al. 2000) but also in purple bacteria (Kennis et al. 1997b; Permentier et al. 2000b). These multi-authored papers reflect the cooperativity and the comradery that Jan perpetuated amongst us all.

Unfortunately, my PhD period ended on a very sad note. Around the time, Sigi and I finished our theses, Jan had notified us that he was seriously ill with lung cancer. We could still finish all the chapters in my thesis, for which I am very grateful to Jan. However, my official PhD ceremony came too late since Jan had passed away a month before the date in early 2001. I have moved away from photosynthesis research but have worked in analytical science ever since. Jan has been a defining figure in my scientific career. We all miss him.

Frank Kleinherenbrink (e-mail: frankkleinherenbrink@outlook.com)

I became Jan Amesz's PhD student in the Biophysics section of the University of Leiden in 1988. I was young, had a degree in Physics, and the reason I applied for the position was that it involved tinkering with lasers. I knew very little -if anything- about photosynthesis at the time, but this did not stop Jan from taking me on. He patiently showed me the way into photosynthesis research and put me to work on the fairly recently discovered heliobacteria (see e.g., van de Meent et al. 1990). I vividly recall the many sessions I had with him in his office in which he typically spent his time with the door closed. Although the continuous presence of his cigarette (sometimes cigar) smoke could be a nuisance, his sharp mind and (very) dry humor always made these sessions a good experience for me. We would review the data I brought him from downstairs in the spectrometer-room where I would fire lasers at photosynthetic bacteria and measure absorption difference kinetics and spectra. Jan often managed to find interesting details and anomalies in data that I considered useless, and amongst other topics we investigated what appeared to be 'uphill' energy transfer from the long wavelength absorbing pigments to the reaction center (see: Kleinherenbrink et al. 1992; Otte et al. 1993). In addition, we (Kleinherenbrink and Amesz 1993) provided critical information on the rates of forward and backward electron transfer at the reaction center in what

at the time was called *Heliobacterium chlorum*. Jan also connected me with other scientists and labs in the field which led to interesting international collaborations (see, e.g., Kleinherenbrink et al. 1993, for collaborating with Bob Blankenship; see his Reminiscences) and to what I consider some of the best work I had the pleasure to be involved with in those years.

In my recollection Jan only very rarely came down to the lab rooms where we did the experimental work; he sort of 'reigned' from his office upstairs and left the technical details to us students and the support staff; however, I never saw this as an issue. Jan's strength as I saw it was really in reviewing the data, drawing conclusions (and asking new questions) from them, and in helping us write them up. Especially on that last point I learned a LOT from him. I can still recall how he would patiently correct my papers with a red pen, and how he often literally cut them up in pieces with scissors. Some of these pieces would end up on the floor, others would be taped back together in order to improve the logic for the flow of the story. This is how I learned to write, and how to build an argument. Even though I did not stay in academia, I have benefited greatly from his lessons in my later career as a scientist in the food industry. At this very moment I am changing career to become a physics teacher myself. Jan certainly was one of the teachers who inspired me over the years, and I remember him fondly. We all miss him.

Robert E. Blankenship (e-mail: reblankenship@gmail.com)

Both Jan Amesz and I worked, for years, on photosynthesis of similar organisms, including *Chloroflexus* and *Heliobacterium*. Jan was a very established biophysicist and his lab had tremendous technical capabilities. He was always very friendly to me at conferences and recognized well my research in his papers and talks that he gave.

One time I went to a conference in Amsterdam (The Netherlands) and met Frank Kleinherenbrink, one of Jan's graduate students. He was doing fluorescence experiments on *Rhodopseudomonas viridis*, which has BChl *b*. At that time, Jan's instrument could not measure fluorescence on the picosecond time scale in the long wavelength region, but we did have that capability at that time in my lab. I invited Frank to come to my lab and do those experiments. Jan agreed and Frank visited and did the experiments, and we published a nice paper that included Jan as a co-author (Kleinherenbrink et al. 1993). Frank came again to my lab as a postdoctoral associate. This was followed, in 1995, by Jan writing a thorough review on the 'The antenna reaction center complex of heliobacteria' for a book that I was editing (see Amesz 1995). In addition, Paula van Noort, another student of Jan's came to work with me as a postdoctoral fellow; for an example of work she did with Jan, see van Noort et al. (1994), and for work with me, see van Noort et al. (1997). Thus, we had a very close connection with Jan and his group, but then sadly he died soon after in 2001.

Jan Amesz was always very even tempered and had a kind of flat way of speaking. I think that may have somewhat limited his impact on others' mind, although his published work was always very clear and of the highest quality.

Unfortunately, Jan was a very heavy smoker for many years, which almost certainly contributed to his early death when he was only 67 years old. However, at some point, he had decided to stop smoking and just quit cold turkey and said that he didn't miss it. I guess it was too late and the damage was already done. We all miss Jan very much."

Suleyman Allakhverdiev (e-mail: Suleyman.allakhverdiev@gmail.com)

During 1986–1992, we had a joint grant (INTAS) between the Pushchino Institute (Institute of Photosynthesis, currently, the Institute of Basic Biological Problems) and the Leiden University (The Netherlands). It was an exchange program and I, with my supervisors Academician Vladimir (Vlad) Shuvalov (see: Vasilieva et al. 2022) and Professor Vyacheslav (Slava) Klimov (Allakhverdiev et al. 2018), visited several times Leiden. It was during that time that I met Jan Amesz, as well as Arnold Hoff, Hans van Gorkom, and Thijs Aartsma, in the Department of Biophysics there. Prof. Amesz, who not only enabled his students to unravel the mysteries of photosynthesis, but also led them into the beautiful world with simplicity, trust, courage, and forgiveness. He was an excellent teacher, a sympathetic mentor, an innovative researcher, and above all, one of the greatest biophysicists of photosynthesis. I do not have sufficient words to describe the superb qualities of Jan Amesz."

Alexandrina Stirbet (e-mail: sstirbet@gmail.com)

My recollections about Jan Amesz are indirect, as I did not have a personal contact with him. However, from 1992 to 1997, the Laboratory of Biophysics at the Faculty of Physics of the University of Bucharest in Romania, where I was working as a researcher, had a collaboration with his laboratory in Leiden (The Netherlands), which was financed by the European Union (EU). Already during the 1989 and 1990 period, the political regimes in several countries, including Romania, in Eastern and Central Europe had dramatically changed–opened up for collaboration. Further, the Council of the European Communities had approved on May 7, 1990,

a trans-European mobility scheme for university studies (labeled as Tempus). Thus, these countries became eligible for economic aid in the higher education domain, including Individual Mobility Grants to students and individuals working in the higher education sector.

Tempus activities allowed multi-lateral cooperation projects, and our laboratory in Bucharest (Romania) started, in 1992, a collaboration with three universities from Portugal, France, and The Netherlands. This resulted in many Mobility Grants received by our students, as well as by several of my colleagues with didactic responsibilities. Between the last ones, two lecturers, Doina Gazdaru and Laura Tugulea, visited The Netherlands to supervise our Romanian students in biophysics multiple times between 1992 and 1997. What I know is that these two colleagues were extremely well received by Professor Jan Amesz and his collaborators in Leiden. In addition, our laboratory also received special financing from EU to purchase scientific equipment, books, and materials for experimental studies. Before I left Romania, in 1993, to stay for a few years in Switzerland, my research profited greatly from the instruments and chemicals that we had received early on, in 1991, from Jan Amesz's laboratory. Further, two computers, from this gift through Jan Amesz, were especially useful for me: an old Apple computer, and a PC/XT, which was the second model in the IBM Personal Computer line. My work with these computers helped me to easily adapt to the task of modeling chlorophyll *a* fluorescence induction (the OJIP curve) when I started to work in Reto Jörg Strasser's Bioenergetics Laboratory in the Department of Biology at the University of Geneva, in Petit Lullier, Switzerland (see Stirbet et al. 1995)."

Richard Cogdell (e-mail: Richard.Cogdell@glasgow.ac.uk)

I first got to know Jan Amesz in the late 1970s. He was part of the famous Biophysics Laboratory at the University of Leiden, in the Netherlands. We had a common interest in trying to understand photosynthetic light harvesting. He quickly became one of those people I would especially look out for whenever I went to conferences on photosynthesis. Jan was a very generous collaborator and I sent several of my co-workers, including Alastair Gardiner, to do experiments in his laboratory in Leiden. As a result of this we published several papers together. For example, Deinum et al. (1989) and Kramer et al. (1995) provided in-depth information on the excitation energy migration steps in the photosynthetic light harvesting antenna of *Rhodopseudomonas acidophila*, and *Rhodopseudomonas cryptolactis*, respectively. During this period, we became good friends. I have many lovely memories of evenings spent eating and drinking with Jan. He had a wonderful, dry sense of humor that always made these evenings full of fun. One of the very worse things about getting old is that you start to lose good friends. I miss Jan both scientifically and as a friend."

Győző Garab (e-mail: garab.gyozo@brc.hu)

Jan Amesz spent a few months in Szeged, Hungary, in 1975, upon the invitation of Ágnes Faludi Dániel. I vividly remember the date (September 10, 1975) as it was when Poland, which had a very good football team, was beating the great Dutch team 4 to 1; Jan and I watched the game in our home. Despite the defeat of Holland, we had a pleasant

Fig. 8 A group photograph at the "Energy Structure & Function (ESF) Advanced School on Spectroscopic Methods in Energy Converting Membranes", held from August 31 to September 14, 1993, at the Biological Research Center, Szeged, Hungary. Jan Amesz is sitting in the middle (6th from right); sitting on his left, János Lányi, Huub de Groot and Leonas Valkunas, and on his right, Győző Garab, Balázs Szalontai, Arnold Hoff and Werner Mäntele—in the company of other, internationally renowned lecturers and teachers of the laboratory practicals, and the students of the school (many of them have become excellent scientists)

Fig. 9 A 1980 photograph of three friends at a Photosynthesis Conference. Left to right: Govindjee; Jan Amesz; and David C. Fork (reproduced from Govindjee et al. 2023; with permission)

Fig. 10 Jan Amesz relaxing with his research group during a 'break" at the 10th *International Symposium on Phototrophic Prokaryotes* in Barcelona, held in August 2000. Left to right: Sigi Neerken; Jan Amesz; Frank Nowak; and Hjalmar Permentier. It appears Jan is telling a story about the fruit he has in his hand, and others are enjoying it. Source: Bas Amesz; caption by: Hjalmar Permentier

evening—luckily, Jan liked the Hungarian wines. It was during this time that I helped Jan and Ágnes by fabricating a sample holder for measuring low-temperature absorbance transients and had the opportunity to discuss with Jan about my research on the composite band-structure of the 77 K fluorescence emission spectra of greening maize chloroplasts (Garab et al. 1974). I also visited Jan in Leiden on one of my international research trips returning from Saclay (France) to Szeged, Hungary somewhen in the early 1980s. Jan also supported our activities in the ESF (European Science Foundation) Programme on "Biophysics of Photosynthesis", 1993–2000. From my perspective, it was then the most efficient network in the life of the European photosynthesis community, with many meetings and schools. Jan was one of its directors (together with Arnold Hoff, Balázs Szalontai and myself). See Fig. 8 for a group photograph from that time. During that school and numerous meetings I often had the privilege to talk to Jan about our work and life in Szeged and Hungary.

Jan showed great interest in our results on circular dichroism (CD) and linear dichroism (LD) of thylakoid membranes and lamellar aggregates of LHCII—and he invited me to write a chapter (Garab 1996) on these techniques in the book "Biophysical Techniques in Photosynthesis" he was editing together with Arnold Hoff. The scientific community will always remember Jan's invaluable contributions to our understanding of the '*Light Reactions of Photosynthesis*'. Many of us will cherish memories about Jan, whose deep knowledge and sharp questions were combined with open-mindedness and helpfulness.

Epilog

We remember Jan Amesz as a great friend to us all. Thus, we end this tribute to him with his photograph with two of his friends from the USA: Govindjee (one of the authors) and the late David C. Fork (Fig. 9); and with some of his coworkers at Leiden University (Fig. 10).

Acknowledgements We thank Hans van Gorkom for providing us contacts with Jan Amesz's family. We also thank Hans Amesz, Jan's brother, for checking and editing the "Introduction" part of this Tribute. We are highly grateful to Robert E, Blankenship for checking the final revised copy before its submission.

Author contributions Govindjee initiated the idea of writing this *In Memoriam* article on the life and research contributions of Jan Amesz, and drafted his research contributions; Bas Amesz drafted the Introduction, which was edited by Govindjee; Győző Garab revised, and edited the research contribution part of the paper; and Alexandrina Stirbet prepared the key figures (Figs. 3 and 4) and checked the entire manuscript, including the references, before the submission of this paper.

Declarations

Competing interests The authors declare no competing interests.

References

Allakhverdiev SI, Zharmukhamedov SK, Rodionova MV, Shuvalov VA, Dismukes C, Shen J-R, Barber J, Samuelsson G, Govindjee G (2018) Vyacheslav (Slava) Klimov (1945–2017): a scientist par excellence, a great human being, a friend, and a Renaissance man. Photosynth Res 136:1–16. https://doi.org/10.1007/s11120-017-0440-5

Amesz J (1963) Kinetics, quantum requirement and action spectrum of light-induced phosphopyridine nucleotide reduction in *Rhodospirillum rubrum* and *Rhodopseudomonas spheroides*. Biochim Biophys Acta 66:22–36. https://doi.org/10.1016/0006-3002(63)91164-8

Amesz J (1964a) Spectrophotometric evidence for the participation of a quinone in photosynthesis of intact blue-green algae. Biochim Biophys Acta 79:257–265

Amesz J (1973) The function of plastoquinone in photosynthetic transport. Biochim Biophys Acta 301:35–51. https://doi.org/10.1016/0304-4173(73)90011-6

Amesz J (1989) Biophysical studies of photosynthesis: Capture and storage of quantum energy in Photosynthesis. In: Briggs WR (ed) Proceedings of the CS French symposium on Photosynthesis held in Stanford, CA, July 17−23, 1988; xxii + 524 pages): photosynthesis (Vol. 8 in the series Plant Biology), Alan R. Liss, Inc., NY, see pp 123–133

Amesz J (1991) Green photosynthetic bacteria and heliobacteria. In: Barton LL, Shively JM (eds) Variations in autotrophic life. Academic Press, London, pp 99–119

Amesz J (1995) The antenna reaction center complex of heliobacteria. In: Blankenship RE, Madigan MT, Bauer CE (eds) Anoxygenic photosynthetic bacteria. Springer, Kluwer, pp 687–697

Amesz J, de Grooth B (1976) Photosynthetic electron transport and electrochromic effects at sub-zero temperatures. Biochim Biophys Acta 440:301–313. https://doi.org/10.1016/0005-2728(76)90064-5

Amesz J, Duysens LNM (1962) Action spectrum kinetics and quantum requirement of phosphopyridine nucleotide reduction and cytochrome oxidation in the blue-green alga *Anacystis nidulans*. Biochim Biophys Acta 64:261–278. https://doi.org/10.1016/0006-3002(62)90736-9

Amesz J, Fork DC (1967) The function of P700 and cytochrome f in the photosynthetic reaction center of system 1 in red algae. Photochem Photobiol 6(12):903–912. https://doi.org/10.1111/j.1751-1097.1967.tb09655.x

Amesz J, Hoff AJ (1996) Biophysical techniques in photosynthesis. Advances in photosynthesis, vol 3. Springer, Dordrecht

Amesz J, van Gorkom HJ (1978) Delayed fluorescence in photosynthesis. Annu Rev Plant Physiol 29:47–66. https://doi.org/10.1146/annurev.pp.29.060178.000403

Amesz J, Visser JWM (1971) Light-induced shifts in pigment absorption in green, red, and blue-green algae. Biochim Biophys Acta 234:62–69. https://doi.org/10.1016/0005-2728(71)90130-7

Amesz J, Vredenberg WJ (1966) Near-infrared action spectra of fluorescence, cytochrome and shift in carotenoid absorption in purple bacteria. Biochim Biophys Acta 126:254–261. https://doi.org/10.1016/0926-6585(66)90061-6

Amesz J, Visser JWM, van den Engh J, Dirks MP (1972) Reaction kinetics of intermediates of the photosynthetic chain between the two photosystems. Biochim Biophys Acta 256:370–380. https://doi.org/10.1016/0005-2728(72)90067-9

Amesz J, Visser JWM, Dirks MP, van den Engh J (1971) Kinetics of plastoquinone and other intermediates of the photosynthetic chain. In: Broda E, Locker A (eds) Proc First European Biophysics Congress, Baden, 14–17 Sep 1971, Vol 4, Wiener Medizischen Akademie. pp 73–77

Amesz J (1964b) Intracellular reactions of nicotinamide-dinucleotide in photosynthetic organisms. Dissertation: University of Leiden, Druk: V.R.B., Groningen

Amesz J (1987) Photosynthesis. In the series: New Comprehensive Biochemistry, vol 15, Elsevier, Amsterdam

Azai C, Tsukatani Y, Itoh S, Oh-oka H (2010) C-type cytochromes in the photosynthetic electron transfer pathways in green sulfur bacteria and heliobacteria. Photosynth Res 104:189–199. https://doi.org/10.1007/s11120-009-9521-4

Blankenship RE (2021) Molecular mechanisms of photosynthesis, 3rd edn. Wiley, Hoboken

Blankenship RE, Madigan M, Bauer C (1995) Anoxygenic Photosynthetic Bacteria Advances in Photosynthesis and Respiration, vol 2. Springer, Cham

Bouges-Bocquet B (1973) Electron transfer between the two photosystems in spinach chloroplasts. Biochim Biophys Acta 314:250–256. https://doi.org/10.1016/0005-2728(73)90140-0

De Grooth BG, Amesz J (1977) Electrochromic absorbance changes of photosynthetic pigments in *Rhodopsuedomomas sphaeroides* I. Stimulation by secondary electron transport at low temperature. Biochim Biophys Acta 462:237–246. https://doi.org/10.1016/0005-2728(77)90122-0

Deinum G, Aartsma TJ, van Grondelle R, Amesz J (1989) Singlet-singlet excitation annihilation measurements on the antenna of *Rhodospirillum rubrum* between 300 and 4 K. Biochim Biophys Acta 976:63–69. https://doi.org/10.1016/S0005-2728(89)80189-6

Duysens LNM (1989) The discovery of the two photosynthetic systems: a personal account. Photosynth Res 21:61–80. https://doi.org/10.1007/BF00033361

Duysens LNM, Amesz J (1957) Fluorescence spectrophotometry of reduced phosphopyridine nucleotide in intact cells in the near-ultraviolet and visible region. Biochim Biophys Acta 24:19–26. https://doi.org/10.1016/0006-3002(57)90141-5

Duysens NM, Amesz J (1959) Quantum requirement for phosphopyridine nucleotide reduction in photosynthesis. Plant Physiol 34:210–213. https://doi.org/10.1104/pp.34.3.210

Duysens LNM, Amesz J (1962) Function and identification of two photochemical systems in photosynthesis. Biochim Biophys Acta 64:243–260. https://doi.org/10.1016/0006-3002(62)90735-7

Duysens LNM, Amesz J, Kamp BM (1961) Two photochemical systems in photosynthesis. Nature 190:510–511. https://doi.org/10.1038/190510a0

Duysens LNM, Amesz J (1967) Photosynthesis. In: Florkin M, Stotz EH (eds), Comprehensive Biochemistry, Vol. 27, "Photobiology and Ionizing Radiation", Chap. 7, Elsevier Publ Co., Amsterdam, pp 237–266

Francke C, Amesz J (1997) Isolation and pigment composition of the antenna system of four species of green sulfur bacteria. Photosynth Res 52:137–146. https://doi.org/10.1023/A:1005845828676

Francke C, Otte SCM, Miller M, Amesz J, Olson JM (1996) Energy transfer from carotenoid and FMO-protein in subcellular preparations from green sulfur bacteria. Spectroscopic characterization of an FMO-reaction center core complex at low temperature. Photosynth Res 50:71–77. https://doi.org/10.1007/BF00018222

Garab G (1996) Linear and circular dichroism. In: Amesz J, Hoff AJ (eds) Biophysical techniques in photosynthesis. Advances in photosynthesis, vol 3. Kluwer, Dordrecht, pp 11–40

Garab G, Horváth G, Faludi-Dániel A (1974) Resolution of the fluorescence bands in greening chloroplasts of maize. Biochem Biophys Res Commun 56:1004–1009. https://doi.org/10.1016/s0006-291x(74)80288-3

Govindjee G (2023) On the evolution of the concept of two light reactions and two photosystems for oxygenic photosynthesis: a personal perspective. Photosynthetica 61:37–47. https://doi.org/10.32615/ps.2023.006

Govindjee G, Pulles MPJ (2016) Louis Nico Marie Duysens (March 15, 1921-September 8, 2015): a leading biophysicist of the 20th century. Photosynth Res 128:223–234. https://doi.org/10.1007/s11120-016-0256-8

Govindjee G, Amesz J, Fork DC (eds) (1986) Light emission by plants and bacteria. Academic Press, Orlando

Govindjee G, Knox RS, Amesz J (1996) Editorial on "Photosynthetic Reaction Centers", a special issue of "Photosynthesis Research"

dedicated to William A. Arnold. Volume 48 (Numbers 1 and 2, May 1996: 1–319. Photosynth Res 48:1–2

Govindjee G, Peterson LF, Satoh K, Herbert H, de Kouchkovsky Y, Schreiber U, Murata N, Öquist G, Larkum AWD, Hiyama T, Berry JA (2023) David (Dave) Charles Fork (1929–2020): a gentle human being, a great experimenter, and a passionate researcher. Photosynth Res 155:107–125. https://doi.org/10.1007/s11120-022-00964-1

Hill R, Bendall F (1960) Function of the two cytochrome components in chloroplasts: a working hypothesis. Nature 186:136–137. https://doi.org/10.1038/186136A0

Hoff AJ, Aartsma TJ (2002) Obituary: Jan Amesz. Photosynth Res 71:104. https://doi.org/10.1023/A:1014931827961

Hoff AJ, Aartsma TJ (2001) Jan Amesz (11.03.1934–29.01.2001) Biochim Biophys Acta 1507:3–4

Kanda T, Ishikita H (2023) Energetic diversity in the electron-transfer pathways of type I photosynthetic reaction centers. Biochemistry 62(4):934–941. https://doi.org/10.1021/acs.biochem.2c00689

Karapetyan NV, Swarthoff T, Rijgersberg CP, Amesz J (1980) Fluorescence emission spectra of cells and subcellular preparations of a green photosynthetic bacterium. Effects of dithionite on the intensity of the emission bands. Biochim Biophys Acta 593:254–260. https://doi.org/10.1016/0005-2728(80)90063-8x

Kennis JTM, Streltsov AM, Aartsma TJ, Nozawa T, Amesz J (1996) Energy transfer and exciton coupling in isolated B800–850 complexes of the photosynthetic purple sulfur bacterium *Chromatium tepidum*. The effect of structural symmetry on bacteriochlorophyll excited states. J Phys Chem 100:2438–2442. https://doi.org/10.1021/jp952475w

Kennis JTM, Streltsov AM, Vulto SIE, Aartsma TJ, Nozawa T, Amesz J (1997a) Femtosecond dynamics in isolated LH2 complexes of various species of purple bacteria. J Phys Chem B 101:7827–7834. https://doi.org/10.1021/jp963359b

Kennis JTM, Streltsov AM, Permentier H, Aartsma TJ, Amesz J (1997b) Exciton coherence and energy transfer in the LH2 antenna complex of *Rhodopseudomonas acidophila* at low temperatures. J Phys Chem B 101:8369–8374. https://doi.org/10.1021/jp971497a

Kim JW, Nguyen-Phan TC, Gardiner AT, Yoon TH, Cogdell RJ, Cho M, Scholes GD (2022) Vibrational modes promoting exciton relaxation in the B850 band of LH2. J Phys Chem Lett 13:1099–1106. https://doi.org/10.1021/acs.jpclett.1c03868

Kleinherenbrink FAM, Amesz J (1993) Stoichiometries and rates of electron transfer and charge recombination in *Heliobacterium chlorum*. Biochim Biophys Acta 1143:77–83. https://doi.org/10.1016/0005-2728(93)90218-5

Kleinherenbrink FAM, Deinum G, Otte SCM, Hoff AJ, Amesz J (1992) Energy transfer from long-wavelength antenna bacteriochlorophylls to the reaction center. Biochim Biophys Acta 1099:175–181. https://doi.org/10.1016/0005-2728(92)90216-O

Kleinherenbrink FA, Cheng P, Amesz J, Blankenship RE (1993) Lifetimes of bacteriochlorophyll fluorescence in *Rhodopseudomonas viridis* and *Heliobacterium chlorum* at low temperatures. Photochem Photobiol 57(1):13–18. https://doi.org/10.1111/j.1751-1097.1993.tb02247.x

Kobayashi M, Watanabe T, Ikegami I, van de Meent EJ, Amesz J (1991) Enrichment of bacteriochlorophyll g' in membranes of Heliobacterium chlorum by ether extraction. Unequivocal evidence for its existence in vivo. FEBS Lett 284:129–131. https://doi.org/10.1016/0014-5793(91)80778-2

Kobayashi MEJ, Van De Meent H, Oh-oka K, Inoue Y, Itoh S, Amesz J, Watanabe T (1992) Pigment composition of heliobacteria and green sulfur bacteria. In: Murata N (ed) Research in photosynthesis, vol I. Kluwer, Dordrecht, pp 393–396

Kraan GP-B, Amesz J, Velthuys BR, Steemers R-G (1970) Studies on the mechanisms of delayed and stimulated fluorescence of chloroplasts. Biochim Biophys Acta 223:129–145. https://doi.org/10.1016/0005-2728(70)90138-6

Kramer HJM, Amesz J (1982) Anisotropy of the emission and absorption bands of spinach chloroplast measured by fluorescence polarization and polarized excitation spectra at low temperature. Biochim Biophys Acta 682:201–207. https://doi.org/10.1016/0005-2728(82)90099-8

Kramer HJM, Amesz J (1996) Antenna organization in the purple sulfur bacteria *Chromatium tepidum* and *Chromatium vinosum*. Photosynth Res 49:237–244. https://doi.org/10.1007/BF00034784

Kramer H, Deinium G, Gardiner AT, Cogdell RJ, Francke C, Aartsma TJ, Amesz J (1995) Energy transfer in the photosynthetic antenna system of the purple non-sulfur bacterium *Rhodopseudomonas cryptolactis*. Biochim Biophys Acta 1231:33–40. https://doi.org/10.1016/0005-2728(95)00065-Q

Miller M, Aartsma TJ, Blankenship RE (2002) Special issue in honor of Jan Amesz: green and heliobacteria—introduction. Photosynth Res 71:1–183

Neerken S, Amesz J (2001) The antenna reaction center complex of heliobacteria: composition, energy conversion and electron transfer. Biochim Biophys Acta 1507:278–290. https://doi.org/10.1016/S0005-2728(01)00207-9

Neerken S, Permentier HP, Francke C, Aartsma TJ, Amesz J (1998) Excited states and trapping in reaction center complexes of the green sulfur bacterium *Prosthecochloris aestuarii*. Biochemistry 37:10792–10797. https://doi.org/10.1021/bi9806899

Neerken S, Aartsma TJ, Amesz J (2000a) Pathways of energy transformation in antenna reaction center complexes of *Heliobacillus mobilis*. Biochemistry 39:3297–3303. https://doi.org/10.1021/bi992433o

Neerken S, Ma YZ, Aschenbrücker J, Schmidt KA, Nowak FR, Permentier HP, Aartsma TJ, Gillbro T, Amesz J (2000b) Kinetics of absorbance and anisotropy upon excited state relaxation in the reaction center core complex of a green sulfur bacterium. Photosynth Res 65:261–268. https://doi.org/10.1023/a:1010647205220

Nuijs AM, Vasmel H, Joppe HL, Duysens LNM, Amesz J (1985a) Excited states and primary charge separation in the pigment system of the green photosynthetic bacterium *Prosthecochloris aestuarii* as studied by picosecond absorbance difference spectroscopy. Biochim Biophys Acta 807:24–34. https://doi.org/10.1016/0005-2728(85)90049-0

Nuijs AM, van Dorssen RJ, Duysens LNM, Amesz J (1985b) Excited states and primary photochemical reactions in the photosynthetic bacterium *Heliobacterium chlorum*. Proc Natl Acad Sci USA 82:6865–6868. https://doi.org/10.1073/pnas.82.20.6865

Nuijs AM, Vasmel H, Duysens LNM, Amesz J (1986) Antenna and reaction-center processes upon picosecond-flash excitation of membranes of the green photosynthetic bacterium *Chloroflexus aurantiacus*. Biochim Biophys Acta 849:316–324. https://doi.org/10.1016/0005-2728(86)90143-X

Otte SCM, Van Der Heiden JC, Pfennig N, Amesz J (1991) A comparative study of the optical characteristics of intact cells of photosynthetic green sulfur bacteria containing bacteriochlorophyll *c*, *d* or *e*. Photosynth Res 28:77–87. https://doi.org/10.1007/BF00033717

Otte SCM, Kleinherenbrink FAM, Amesz J (1993) Energy transfer between the reaction center and the antenna in purple bacteria. Biochim Biophys Acta 1143:84–90. https://doi.org/10.1016/0005-2728(93)90219-6

Permentier HP, Schmidt KA, Kobayashi M, Akiyama M, Braun CH, Neerken S, Miller M, Amesz J (2000a) Composition and optical properties of reaction centre core complexes from the green sulfur bacteria *Prosthecochloris aestuarii* and *Chlorobium tepidum*. Photosynth Res 64(1):27–39. https://doi.org/10.1023/A:1026515027824

Permentier HP, Neerken S, Schmidt KA, Overmann J, Amesz J (2000b) Energy transfer and charge separation in the purple non-sulfur bacterium *Roseospirillum parvum*. Biochim Biophys Acta 1460:338–345. https://doi.org/10.1016/s0005-2728(00)00200-0

Rijgersberg CP, Amesz J, Thielen APGM, SwagerJ A (1979) Fluorescence emission spectra of chloroplasts and subchloroplast preparations at low temperatures. Biochim Biophys Acta 545:473–482. https://doi.org/10.1016/0005-2728(79)90156-7

Rijgersberg C, van Grondelle R, Amesz J (1980) Energy transfer and bacteriochlorophyll fluorescence in purple bacteria at low temperature. Biochim Biophys Acta 592:53–64. https://doi.org/10.1016/0005-2728(80)90113-9

Romijn JC, Amesz J (1976) Photochemical activities of reaction centers from *Rhodopseudomonas sphaeroides* at low temperature and in the presence of chaotropic agents. Biochim Biophys Acta 423:164–173. https://doi.org/10.1016/0005-2728(76)90175-4

Schmidt KA, Neerken S, Permentier HP, Hager-Braun C, Amesz J (2000) Electron transfer in reaction center core complexes from the green sulfur bacteria *Prosthecochloris aestuarii* and *Chlorobium tepidum*. Biochemistry 39:7212–7220. https://doi.org/10.1021/bi992861u

Shuvalov V, Amesz J, Duysens LNM (1986) Picosecond spectroscopy of isolated membranes of the photosynthetic green sulfur bacterium *Prosthecochloris aestuarii* upon selective excitation of the primary electron donor. Biochim Biophys Acta 851:1–5. https://doi.org/10.1016/0005-2728(86)90242-2

Smit HWJ, Amesz J, van der Hoeven MFR (1987) Electron transport and triplet formation in membranes of the photosynthetic bacterium *Heliobacterium chlorum*. Biochim Biophys Acta 893:232–240. https://doi.org/10.1016/0005-2728(87)90044-2

Steensgaard DB, van Walree CA, Permentier HP, Baneras L, Borrego CM, Garcia GJ, Aartsma TJ, Amesz J, Holzwarth AR (2000) Fast energy transfer between BChl it d and BChl c in chlorosomes of the green sulfur bacterium *Chlorobium limicola*. Biochim Biophys Acta 1457(1–2):71–80

Stirbet A, Govindjee G, Strasser BJ, Strasser RJ (1995) Numerical simulation of chlorophyll *a* fluorescence induction in plants. In: Mathis P (ed) Photosynthesis: from light to biosphere, vol II. Kluwer Academic Publishers, The Netherlands, pp 919–922

Swarthoff T, Amesz J (1979) Photochemically active pigment-protein complexes from the green photosynthetic bacterium *Prosthecochloris aestuarii*. Biochim Biophys Acta 548:427–432. https://doi.org/10.1016/0005-2728(79)90146-4

Swarthoff T, Amesz J, Kramer HJM, Rijgersberg P (1981) The reaction center and antenna pigments of green photosynthetic bacteria. Isr J Chem 21:332–337. https://doi.org/10.1002/ijch.198100060

Swarthoff T, Kramer HJM, Amesz J (1982) Thin-layer chromatography of pigments of the green bacterium *Prosthecochloris aestuarii*. Biochim Biophys Acta 681:354–358. https://doi.org/10.1016/0005-2728(82)90175-X

van de Meent EJ, Kleinherenbrink FAM, Amesz J (1990) Purification and properties of an antenna-reaction center complex from heliobacteria. Biochim Biophys Acta 1015:223–230. https://doi.org/10.1016/0005-2728(90)90024-X

van de Meent EJ, Kobayashi M, Erkelens C, van Veelen PA, Amesz J (1991) Identification of 8^1-hydroxychlorophyll *a* as a functional reaction center pigment in heliobacteria. Biochim Biophys Acta 1058:356–362. https://doi.org/10.1016/S0005-2728(05)80131-8

van de Meent EJ, Kobayashi M, Erkclens C, van Veelen PA, Otte SCM, Inoue K, Watanabe T, Amesz J (1992) The nature of the primary electron acceptor in green sulfur bacteria. Biochim Biophys Acta 1102(3):371–378. https://doi.org/10.1016/0005-2728(92)90137-Q

van Dorssen RJ, Amesz J (1988) Pigment organization and energy transfer in the green photosynthetic bacterium *Chloroflexus aurantiacus*. III. Energy transfer in whole cells. Photosynth Res 15:177–189. https://doi.org/10.1007/BF00035261

van Grondelle R, Amesz J (1986) Excitation energy transfer in photosynthetic systems. In: Amesz J, Fork DC, Govindjee G (eds) Light emission by plants and bacteria. Academic Press Inc, New York, pp 191–224

van Grondelle R, van Gorkom H (2014) The birth of the photosynthetic reaction center: the story of Lou Duysens. Photosynth Res 120:3–7. https://doi.org/10.1007/s11120-013-9959-2

van Dorssen RJ, Vasmel H, Amesz J (1985) Antenna organization and energy transfer in membranes of *Heliobacterium chlorum*. Biochim Biophys Acta 809:199–203. https://doi.org/10.1016/0005-2728(85)90063-5

van Dorssen RJ, Gerola PD, Olson JM, Amesz J (1986a) Optical and structural properties of chlorosomes of the photosynthetic green sulfur bacterium *Chlorobium limicola*. Biochim Biophys Acta 848:77–82. https://doi.org/10.1016/0005-2728(86)90162-3

van Dorssen RJ, Vasmel H, Amesz J (1986b) Pigment organization and energy transfer in the green photosynthetic bacterium *Chloroflexus aurantiacus*. II. The chlorosome. Photosynth Res 9:33–45. https://doi.org/10.1007/BF00029729

van Kan PJM, Aartsma TJ, Amesz J (1989) Primary photosynthetic processes in *Heliobacterium chlorum* at 15K. Photosynth Res 22:61–68. https://doi.org/10.1007/BF00114767

van Noort PI, Gormin DA, Aartsma TJ, Amesz J (1992) Energy transfer and primary charge separation in *Heliobacterium chlorum* studied by picosecond time-resolved transient absorption spectroscopy. Biochim Biophys Acta 1140:15–21. https://doi.org/10.1016/0005-2728(92)90014-S

van Noort PI, Gormin DA, Aartsma TJ, Amesz J (1994) Energy transfer and trapping of excitations in membranes of *Heliobacterium chlorum* at 15 K. Biochim Biophys Acta 1184:21–27. https://doi.org/10.1016/0005-2728(94)90149-X

van Noort PI, Zhu Y, LoBrutto R, Blankenship RE (1997) Redox effect on the excited-state lifetime in chlorosomes and bacteriochlorophyll *c* oligomers. Biophys J 72:316–325. https://doi.org/10.1016/S0006-3495(97)78670-3

Vasilieva LG, Kaminskaya OP, Yakovlev AG, Shkuropatov AY, Semenov AY, Nadtochenko VA, Krasnovsky AA Jr, Parson WW, Allakhverdiev SI, Govindjee G (2022) In memory of Vladimir Anatolievich Shuvalov (1943–2022): an outstanding biophysicist. Photosynth Res 154:207–223. https://doi.org/10.1007/s11120-022-00932-9

Vasmel H, Meiburg RF, Kramer HJM, de Vos LJ, Amesz J (1983) Optical properties of the photosynthetic reaction center of *Chloroflexus aurantiacus* at low temperature. Biochim Biophys Acta 724:333–339. https://doi.org/10.1016/0005-2728(83)90092-0

Velthuys BR, Amesz J (1974) Charge accumulation at the reducing side of system 2 of photosynthesis. Biochim Biophys Acta 333:85–94. https://doi.org/10.1016/0005-2728(74)90165-0

Visser JW, Amesz J, van Gelder BV (1974) EPR signals of oxidized plastocyanin in intact algae. Biochim Biophys Acta 333:279–287. https://doi.org/10.1016/0005-2728(74)90011-5

Vos M, van Grondelle R, van der Kooij FW, van de Poll D, Amesz J, Duysens LNM (1986) Singlet-singlet annihilation at low temperatures in antenna of purple bacteria. Biochim Biophys Acta 850:501–512. https://doi.org/10.1016/0005-2728(86)90119-2

Vos M, Nuijs AM, van Grondelle R, van Dorssen RJ, Gerola PD, Amesz J (1987) Excitation transfer in chlorosomes of green photosynthetic bacteria. Biochim Biophys Acta 891:275–285. https://doi.org/10.1016/0005-2728(87)90222-2

Vredenberg WJ, Amesz J (1966) Absorption bands of bacteriochlorophyll types in purple bacteria and their response to illumination. Biochim Biophys Acta 126:244–261. https://doi.org/10.1016/0926-6585(66)90060-4

Vredenberg WJ, Amesz J, Duysens LNM (1965) Light-induced spectral shifts in bacteriochlorophyll and carotenoid absorption in purple bacteria. Biochem Biophys Res Commun 18:435–439. https://doi.org/10.1016/0006-291x(65)90727-8

Vulto SIE, Neerken S, Louwe RJW, de Baat MA, Amesz J, Aartsma TJ (1998) Excited-state structure and dynamics in FMO antenna complexes from photosynthetic green sulfur bacteria. J Phys Chem B 102:10630–10635. https://doi.org/10.1021/jp983003v

Vulto SIE, de Baat MA, Neerken S, Nowak FR, van Amerongen H, Amesz J, Aartsma TJ (1999a) Excited state dynamics in FMO antenna complexes from photosynthetic green sulfur bacteria: a kinetic model. J Phys Chem B 103:8153–8161. https://doi.org/10.1021/jp984702a

Vulto SIE, Kennis JTM, Streltsov AM, Amesz J, Aartsma TJ (1999b) Energy relaxation within the B850 absorption band of the isolated light-harvesting LH2 from *Rhodopseudomonas acidophila* at low temperature. J Phys Chem B 103:878–883. https://doi.org/10.1021/jp9825415