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TRIBUTE

Remembering Otto Kandler (1920–2017) and his contributions

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Abstract
After a brief prologue on Otto Kandler's life, we describe briefly his pioneering work on photosynthesis (photophosphorylation and the carbon cycle) and his key participation in the discovery of the concept of three forms of life (Archaea, ~~Prokarya~~, and Eukarya). With Otto Kandler's passing, both the international photosynthesis and microbiology communities have lost an internationally unique, eminent, and respected researcher and teacher who exhibited a rare vibrancy and style.

Keywords Archaea · Carbon reactions · Photophosphorylation in vivo · Three forms of life · Carl Woese

Life of Otto Kandler

Otto Kandler, who had served as a professor at Ludwig-Maximilians University in Munich for many years, was born on October 23, 1920 in Deggendorf in Lower Bavaria, and died at the age of 96, on August 29, 2017 in Munich. He developed his interest in Plant Biology before he went to the elementary school. When he was a 12-year-old schoolboy, he was already reading books on the theories of Charles Darwin. This, however, was not accepted by a catholic priest, and he was punished with a wooden stick. In spite of this (and maybe because of this), he became deeply involved with and intrigued by biology and evolution. From 1935 to 1938, he studied at "Aufbauschule" in Straubing, a high school for gifted children who could not afford to attend the gymnasium. After the War in 1946, he received a special high school diploma, which gave him the opportunity to take courses in both biological and physical sciences at the Ludwig Maximilians University (LMU) in Munich. In 1949, he received his doctorate under Karl Suessenguth, for his work on plant tissue cultures which answered important questions in plant metabolism. In 1953, he received his Habilitation from LMU. Already in 1950, Otto Kandler presented the very first experimental evidence in vivo for the existence of photophosphorylation. For these findings he was offered a Rockefeller fellowship. So, a major trip abroad was to USA, where he chose to work on basic questions in photosynthesis in the laboratories of Martin Gibbs and Melvin Calvin (for details, see below).

Several key characteristics of Otto Kandler have been described by one of us (Tanner 2017): He was full of energy and always ready to engage in discussions and had an intense professional involvement in research; at the same time, he was a refined connoisseur of the arts and also very much of a family man. His wife Gertraud, his three daughters, and four grandchildren speak highly of him.

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Research

The research contributions of Otto Kandler, who passed away last year, to plant and microbial biology are enormous. He was a uniquely gifted scientist with a deep understanding of the physiology of plants and bacteria, from the molecular level to the level of the whole plant and the microbes. For a brief obituary, see Renner (2018), and for an in-depth understanding of Otto's contributions, see Schleifer (2011) and Tanner (2017, published in German). In this Tribute,

Fig. 1 Carl Woese (left), Ralph Wolfe (middle), and Otto Kandler (right), celebrating the archaebacteria (now Archaea) on top of Mt. Hochiss in 1981; Photo by Gertraud Kandler; for a few more photographs of Otto Kandler from 1956–1983, see Supplementary Material

we focus on his early work on photosynthesis and then on his insightful and deep involvement with Carl Woese's three forms of life: Archaea, Bacteria, and Eukarya. Figure 1 shows Otto Kandler with Carl Woese and Ralph Wolfe, the pioneers of three forms of life.

On photophosphorylation

A major contribution by Otto Kandler in photosynthesis research was his pioneering work on photophosphorylation in vivo. It was in the early 1950s that he published evidence for the existence of photophosphorylation in vivo (in the green alga Chlorella): i.e., making of ATP from inorganic phosphate [see his four single-authored papers in German (Kandler 1950, 1954, 1955, 1957); the Appendix provides the titles of these papers in English]. We would also like to mention the independent work of Bernie Strehler (1953), who discovered light-induced production of ATP in photosynthetic cells, using luciferin–luciferase system [for this story, see Strehler (1996)]. We all know about the discovery of photophosphorylation by Arnon et al. (1954, 1961) in chloroplasts and by Al Frenkel (1954; see Govindjee and Frenkel 2015 for a tribute to Al Frenkel) in bacterial chromatophores. However, it was after several years of Kandler's original work in the 1950s (cited above, where cell inorganic phosphate was shown to be turned into organic phosphate; see Kandler (1960, 1981) for his views, and for work of others at that time, see Jagendorf 2002; see, Govindjee 2017, for a tribute to Jagendorf). In vivo evidence for the existence of the so-called cyclic photophosphorylation was published later by Kandler and his associates (Tanner et al. 1968, 1969; Klob et al. 1972, 1973).

Tanner et al. (1968, 1969) had considered that their data clearly showed the existence of cyclic photophosphorylation, but they had concluded that it did not stoichiometrically contribute ATP to photosynthetic CO_2 fixation in Chlorella. Klob et al. (1972, 1973) showed that when they inhibited cyclic photophosphorylation in *Chlorella vulgaris* cells by carbonyl cyanide-trifluoromethoxy phenylhydrazone (CCCP), a lag was observed not only in CO_2 fixation, but in the formation of ribulose bisphosphate (RuBP). Otto Kandler and his coworkers made the obvious conclusion that cyclic photophosphorylation must have proceeded to phosphorylate all the key intermediates of the Calvin–Benson–Bassham[1] cycle since, under their experimental conditions, noncyclic photophosphorylation was not in "full gear." Klob et al. (1972) as well as Klob et al. (1973) provided firm evidence for the obligate requirement of cyclic photophosphorylation in vivo under specific experimental conditions during the initial phase of CO_2 fixation.

Further, Kandler and his coworkers showed, for the first time, the existence of ADP-glucose, the glucose donor for the formation of starch (see e.g., Kauss and Kandler 1962). In addition, they noticed that the biosynthesis of the raffinose-type oligosaccharides, galactosides of sucrose, and the main water-soluble saccharides in many plant families follow a complete new pathway. The galactosyl residues are not transferred from UDP-Gal but from galactinol, a galactoside of myo-inositol (Tanner and Kandler 1968).

On the carbon cycle

On a Rockefeller fellowship, Kandler, worked with Martin Gibbs, and with Melvin Calvin from 1956 to 1957. Here, the focus was on the *carbon reactions*. Black (2008) and Black and Govindjee (2009) describe the story of how Kandler came to work with Gibbs in USA. Kandler and Gibbs (1956) and Gibbs and Kandler (1957), working with the green alga *Chlorella* and the leaves of higher plants, showed that glucose had an asymmetric distribution of C-14; this clearly meant, then, that two equal triose phosphates could not give the hexose phosphate, thus, providing a key question (and discussion[2]) for the Calvin–Benson–Bassham cycle (or the carbon reaction cycle). (Cf. Bassham (2003) and Benson

[1] For a tribute to Al Bassham, see Govindjee et al. (2016), and for a tribute to Andy Benson, see Buchanan et al. (2016).

[2] Gibbs and Kandler (1957) had isolated ^{14}C-labeled glucose after a brief time of $^{14}CO_2$-photosynthesis, and degraded it carbon by carbon. They discovered an asymmetric labeling of glucose carbon atoms, which, apparently, did not quite "match" the then formulated Calvin–Benson–Bassham cycle [see Benson (2002; republished in 2005) and Bassham (2003; republished in 2005) on the carbon reduction cycle of photosynthesis]. Ultimately, of course, these issues have been resolved, but history has its own lessons.

(2002) for their stories on the discovery of the entire cycle for which Melvin Calvin received the 1961 Nobel Prize in Chemistry.) It later became clear that an asymmetric ^{14}C-labeling of hexoses during short times of photosynthesis is not really an argument against the C3 photosynthetic carbon reduction cycle. All is well that ends well. The above shows how science progresses.

On three forms of life

We end this Tribute by mentioning that although Carl Woese is usually given all the credit for suggesting that living organisms fall in three groups (Archaea, Bacteria, and Eukarya) instead of two groups (Prokaryotes and Eukaryotes), we emphasize that Otto Kandler's contributions were crucial to this new paradigm (see Woese et al. 1990; Kandler 1998). Kandler and Hippe (1977) had shown that although members of archaebacteria (now Archaea) had several cell wall types, none of them were like those of other bacteria (peptidoglycan type).

Otto Kandler had indeed distinguished himself with extraordinarily exciting work on the evolution and the overall classification of all the organisms into three domains (see above), a reorganization he had designed in collaboration with Carl Woese, a man he had called the "Darwin of the 20th century." It was Kandler who had recognized the importance of Archaea and initiated research in this field in Germany, which brought much attention to it from all over the world.

One wonders as to what was really the thing that got him close to Woese's concepts. Well, for one, he had studied the composition and the primary structure of bacterial "murein," whose diversity he had recognized long ago (Schleifer and Kandler 1972), which led to an improved classification of gram-positive bacteria, but nothing more. However, Kandler and Hippe (1977) discovered the absence of a true murein sacculus in what was then called archaebacteria (now Archaea); this was a significant finding and led to the separation of this group of organisms from bacteria. Further, Kandler discovered that some of the archaea had pseudomurein, which was a novel cell wall component (König and Kandler 1979). For further details, see Sapp (2009).

One of us (G) was enamored by Carl's research and used to drop by in his office that was one floor above Govindjee's in Morrill Hall of the UIUC. He had invited and edited Carl's article (Woese 2004). Woese describes beautifully how, before his own work was published, Kandler encouraged and helped develop the concept of differences between archaebacteria (now Archaea) and other bacteria by organizing the first meeting in 1981 in Munich and editing the manuscripts for "Zentralblatt für Bakteriologie, Mikrobiologie und Hygiene. 1. Abt. Originale C. Allgemeine, Angewandte und ökologische Mikrobiologie."

During this visit of Kandler to Urbana, Govindjee also had an opportunity to chat with him about his pioneering work on photosynthesis, particularly on photophosphorylation. We miss Otto Kandler, one of the greatest biochemists of our times. For further information on Kandler, see Wikipedia at https://en.wikipedia.org/wiki/Otto_Kandler.

Acknowledgements We thank Gertraud (Trudy) Kandler for the photograph in Fig. 1, and for providing us information on Otto Kandler, her husband for 65 years. Further, we are grateful to Maya Kandler for checking the final version of this Tribute and for her valuable suggestions (also see Supplementary Material for photographs of Otto Kandler). Govindjee thanks his son Sanjay Govindjee for helping him in translating German papers into English, and his grandson Rajiv Govindjee for reading this tribute before its publication.

Appendix

For the benefit of the readers who are not familiar with German, we provide below the English translation of the following papers. (See original under references).

Kandler O (1950) On the relationship between the phosphate metabolism and photosynthesis I. Variations in phosphate levels in *Chlorella pyrenoidosa* as a consequence of light-dark changes. Z Naturforsch **5b**:423–437

Kandler O (1954) On the relationship between phosphate metabolism and photosynthesis II. Increases in glucose-uptake/content in light as an indicator of a light dependent phosphorylation. Z. Naturforsch. **9b**:625–644

Kandler O (1955) On the relationship between phosphate balance/budget/content and photosynthesis. III. Inhibition analysis of light dependent phosphorylation. Z Naturforsch **10b**:38–46

Kandler O (1957) On the relationship between phosphate budget and photosynthesis. IV. On the question of a stoichiometric relation between CO_2-reduction and phosphate exchange. Z Naturforsch **12b**:271–280

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Black CC (2008) Martin Gibbs (1922–2006). Pioneer of ^{14}C research, sugar metabolism & photosynthesis; vigilant editor-in-chief of plant physiology; sage educator; and humanistic mentor. Photosynth Res 95:1–10

Black CC, Govindjee (2009) Martin Gibbs and the peaceful uses of nuclear radiation, ^{14}C. Photosynth Res 99:63–80

Buchanan BB, Douce R, Govindjee, Lichtenthaler HK, Summons RE (2016) Andrew Alm Benson, 1917–2015, biographical memoir of the national academy of science, USA 16 pages, available ONLINE

Frenkel A (1954) Light-induced phosphorylation by cell-free preparations of photosynthetic bacteria. J Am Chem Soc 76:5568–5569

Gibbs M, Kandler O (1957) Asymmetric distribution of C-14 in sugars formed during photosynthesis. Proc Natl Acad Sci USA 43:423–437

Govindjee (2017) André Tridon Jagendorf (1926–2017). Photosynth Res 132:235–243

Govindjee, Frenkel S (2015) Albert W. Frenkel (1919–2015): photosynthesis research pioneer, much-loved teacher, and scholar. Photosynth Res 124:243–247

Govindjee, Bassham H, Bassham S (2016) Remembering James Alan Bassham (1922–2012). Photosynth Res 128:3–13

Jagendorf AT (2002) Photophosphorylation and the chemiosmotic perspective. Photosynth Res 73:233–241

Kandler O (1950) Über die Beziehungen zwischen Phosphathaushalt und Photosynthese I: phosphatspiegelschwankungen bei *Chlorella pyrenoidosa* als Folge des Licht-Dunkel-Wechsels. Z Naturforsch 5b:423–437 (**see Appendix for translation in English**)

Kandler O (1954) Über die Beziehungen zwischen Phosphathaushalt und Photosynthese II: gesteigerter Glucoseeinbau im Licht als Indikator einer lichtabhängigen Phosphorylierung. Z Naturforsch 9b:625–644 (**see Appendix for translation in English**)

Kandler O (1955) Über die Beziehungen zwischen Phosphathaushalt und Photosynthese. III. Hemmungsanalyse der Licht abhängigen Phosphorylierung. Z Naturforsch 10b:38–46 (**see Appendix for translation in English**)

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Supplementary Material

for

Remembering Otto Kandler (1920–2017) and his contributions

by

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See the following four pages for photographs of Otto Kandler.

Photographs of Otto Kandler

Five photographs of Otto Kandler, arranged chronologically, are presented below (source: Archives of Otto Kandler's family; provided by Maya Kandler).

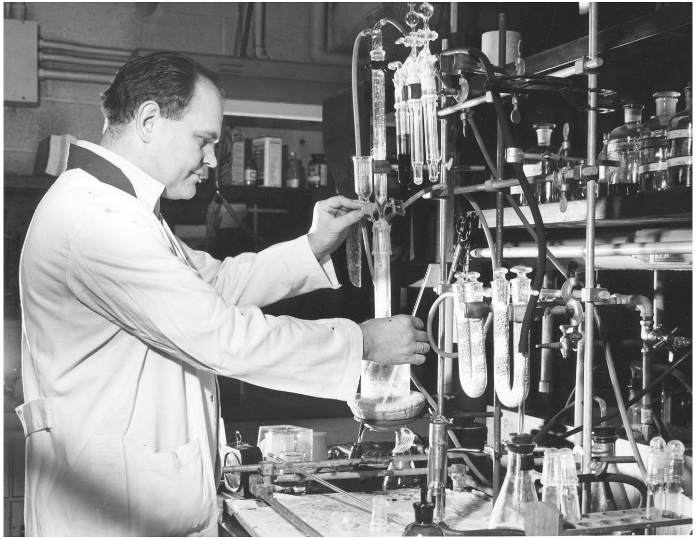

Figure S1. Otto Kandler doing experiments at Brookhaven National Laboratory, USA (1956)

Figure S2. Left to right: Daniel Arnon, Otto Kandler and Gertraud Kandler (1960)

Figure S3. Otto Kandler in his office in Germany (1976)

Figure S4. Left to right: Carl Woese, Otto Kandler and Ralph Wolfe (1981; also see Fig. 2 in the main text)

Figure S5. Otto Kandler in his laboratory in Germany (1983)