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Special issue in honor of Prof. Hartmut Karl Lichtenthaler

HISTORY & BIOGRAPHY

Honoring Hartmut Karl Lichtenthaler, innovative pioneer of photosynthesis, on his 90th birthday

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Abstract

We honor Professor Hartmut Karl Lichtenthaler, a versatile pioneer of photosynthesis research, plant physiology, isoprenoid biochemistry, and stress physiology of plants, for his groundbreaking and creative contributions to plant science. His innovative research on the chemical composition, ultrastructure, and function of chloroplasts and his detection of the major methylerythritol 4-phosphate (MEP) isoprenoid biosynthetic pathway in plants is key to our current understanding of the physiology and biochemistry of photosynthesis systems. His ingenious use of the powerful laser-induced chlorophyll *a* fluorescence imaging has helped us better understand the stress response processes in plant leaves. In this tribute, we present a summary of Lichtenthaler's career, significant scientific contributions, editorial engagement, promotion of international cooperation, many honors, and awards, as well as his devotion to hiking and mountaineering.

Keywords: chlorophyll fluorescence; chloroplast ultrastructure; DOXP/MEP pathway; fluorescence imaging of photosynthetic function; isoprenoid biosynthesis; mode of action of herbicides; phylloquinone K_1; plastoglobuli; sun/shade-type chloroplasts; the Berkeley Spirit.

Life and career

Hartmut Karl Lichtenthaler (Fig. 1) was born on 20 June 1934 in Weinheim (near Heidelberg), Germany. After finishing his school education in 1953 in Heidelberg, he studied botany and pharmacy at the nearby Technical University of Karlsruhe. There he completed his studies in 1958 with the pharmaceutical state examination. He then transferred to the University of Heidelberg, the oldest German University, which was founded in

Highlights

- Lichtenthaler has made defining contributions to DOXP/MEP pathway in plants
- He is a pioneer of chlorophyll fluorescence imaging to detect stress responses in plants
- He is an editor par excellence – who also brought scientists from East and West together

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Fig. 1. A 2019 photograph of Hartmut Lichtenthaler in Karlsruhe, Germany.

1386 (https://www.uni-heidelberg.de/university/history/history.html). He began research for his doctoral thesis in plant physiology on "Vitamin K_1 (phylloquinone) and chlorophylls in green plants" at the institute headed by Professor August Seybold (1901–1965); the latter is well-known for his pioneering and the first exact determination of the individual amounts of chlorophyll (Chl) *a* and *b* as well as of carotenes and xanthophylls in green plants after having successfully separated them by chromatography on sugar columns (Seybold and Egle 1937). In 1961, Hartmut earned his PhD degree from the University of Heidelberg. This was followed by his research, at the Centre d'Études Nucléaires (CEN) de Grenoble, France, on the uptake of phosphate by ^{32}P labeling of plant roots. Soon thereafter (1962–1964), he was a research fellow at the University of California, Berkeley, Laboratory of Chemical Biodynamics, under the Nobel laureate Professor Melvin Calvin (1911–1997; for Calvin, *see* Govindjee *et al*. 2020); there, he worked on the prenyl-quinone and pigment composition of photosynthetic membranes. In 1964, after he returned to Germany, he was appointed Assistant Professor at the University of Münster, Westphalia. After completion of his "Habilitation", in 1967, with the thesis "The function of plastoquinone-9, phylloquinone K_1, α-tocopherol and osmiophilic plastoglobuli in chloroplasts", he was promoted to the position of Associate Professor.

In 1970, Hartmut Lichtenthaler was appointed Full Professor of plant physiology, plant biochemistry, and pharmaceutical biology at the University of Karlsruhe, Germany. There, he developed the institute to become a world-renowned center for photosynthesis research, isoprenoid biochemistry, chlorophyll fluorescence imaging, and the photosynthesis of intact leaves, as well as for stress detection in plants. Hartmut strongly promoted international scientific cooperation and exchange. In following the example of his mentor Melvin Calvin, Hartmut opened his Karlsruhe laboratory to PhD students, postdoctoral fellows, and guest scientists who came from all over the world, both the East and the West. In Hartmut's lab, these guest scientists, including advanced PhD students, who came from 15 different countries on fellowships, arranged by Hartmut, had the opportunity to use modern up-to-date instruments to do their research. (We note that these instruments were not available in their laboratories, especially to those from the Communist countries behind the Iron Curtain.)

Since 2001, Hartmut Lichtenthaler, as Professor Emeritus, has actively continued his versatile research endeavors in photosynthesis and plant biochemistry. In addition, he started to document and write on various historical topics of plant biology. We summarize below some of his research over the years.

Research and major scientific achievements

Hartmut Lichtenthaler's major research, since the 1960s, focused on the functional aspects of photosynthesis, pigment composition, ultrastructure, light-adaptation, biosynthesis, and metabolism in chloroplasts. For basic information on photosynthesis, *see* Blankenship (2021) and Stirbet *et al.* (2020). Hartmut's discoveries include the following: (*1*) Phylloquinone K_1 is specifically bound to Photosystem I and is a component of the photosynthetic electron transport system (Lichtenthaler 1969, Interschick-Niebler and Lichtenthaler 1981). (*2*) The osmiophilic plastoglobuli, found in many electron micrographs of chloroplasts, are not fixation artefacts, but are genuine morphological structures that serve to store chloroplast lipids, in particular plastoquinone-9 and α-tocopherol (vitamin E); further, he found that these compounds accumulate in high amounts in sun-type chloroplasts and chloroplasts of perennial leaves (Lichtenthaler 1968; *see* Lichtenthaler 2007 and 2013 for reviews). (*3*) New information on the light-adaptation response of chloroplasts and on the differences in ultrastructure, thylakoid arrangement, pigment composition, ratios of Chl *a*/*b* and the rates of photosynthesis of the "sun-type chloroplasts" *vs*. "shade-type chloroplasts" – as found in many sun and shade acclimated leaves (Lichtenthaler *et al.* 1981, 1982; Lichtenthaler and Babani 2004).

Further, Hartmut re-determined the specific absorption coefficients of chlorophyll *a* and *b* as well as that of plant leaf carotenoids, suspended in several different organic solvents. From these results, he established the equations which allow us to simultaneously determine the Chl *a* and Chl *b* content as well as the sum of total carotenoids (both xanthophylls and carotenes) in the same leaf extract, using the optical densities, measured just at three different wavelengths (Lichtenthaler 1987, Lichtenthaler and Buschmann 2001, also *see* Lichtenthaler 2007). Today, this method is used for Chl and carotenoid determination worldwide in many laboratories of plant physiology and photosynthesis research (*see e.g.*, Hu *et al.* 2020).

Hartmut is a pioneer in the use of the red and far-red Chl *a* fluorescence in studying the effects of stress on plants and on the photosynthetic apparatus itself (Lichtenthaler 1988). He has emphasized the use of R_{Fd}, *i.e.*, Chl fluorescence decrease ratio, as a monitor of the photosynthetic rates of intact leaves (Lichtenthaler and Rinderle 1988a; *see* also Lichtenthaler 2020). *In vivo*

measurement of Chl *a* fluorescence in intact leaves of herbaceous plants and trees is indeed a powerful method to determine the decline of photosynthetic function and damage to the photosynthetic apparatus by several environmental (including air pollution) stresses and in the decline of forest health (Lichtenthaler and Buschmann 1984a,b; Lichtenthaler and Rinderle 1988b). Using comprehensive eco-physiological field and laboratory approaches, including airborne measurements, done in collaboration with NASA (National Aeronautics and Space Administration), USA, Hartmut and his research group proved that an early decline of photosynthetic function and loss of Chl content, induced by photo-oxidative and photo-inhibitory damage, are indeed the major causes for the large-scale die-off of forest trees in Europe and in the USA (Rock *et al*. 1986, Rinderle and Lichtenthaler 1989; *see* also Sharkey and Govindjee 2016).

Furthermore, Hartmut is the top authority for imaging the red and far-red Chl *a* fluorescence of intact leaves, which allows simultaneous determination, in a non-invasive way, of the individual photosynthetic activity of an enormous number of leaf pixels and the large gradients in photosynthetic activity over the leaf surface (Buschmann and Lichtenthaler 1998, Lichtenthaler and Babani 2000, Lichtenthaler *et al.* 2007a, 2013). This method also permits simultaneous imaging of the blue and green fluorescence of leaves, together with the red and the far-red Chl *a* fluorescence, "Multicolor Fluorescence Imaging", that is well-suited for early stress detection in plants, and allows, *via* particular fluorescence ratios (red/far-red, blue/red, or blue/green) to differentiate between a variety of stress conditions (*see* Lichtenthaler 2021 for a review).

In addition to the above, Hartmut has studied the mode of action of various herbicides and antibiotics active in chloroplasts, such as the inhibitors of photosynthetic electron transport (Pfister *et al*. 1975), but also the inhibitors of the *de novo* fatty acid biosynthesis in chloroplasts. With his research group, Hartmut has detected five enzymes of the *de novo* fatty acid biosynthesis pathway which are the targets and specific inhibition sites of various herbicides and antibiotics (Lichtenthaler *et al.* 1980, Kobek *et al.* 1988, Lichtenthaler 1990, Golz *et al*. 1994).

The DOXP/MEP pathway: Late in his career, Hartmut made another breakthrough discovery in establishing the non-mevalonate, deoxyxylulose-5-phosphate/methylerythritol-4-phosphate (DOXP/MEP) pathway, as the cognizant isoprenoid biosynthesis process in chloroplasts (Fig. 2). This pathway was identified in the 1990s by Hartmut in close cooperation with Michel Rohmer (Fig. 3), when they used ^{13}C to label isoprenoids, and high-resolution NMR spectroscopy to monitor the intermediates of the process (Lichtenthaler *et al.* 1997, Lichtenthaler 1999, 2007). Evidence in support of the DOXP/MEP pathway in chloroplasts was in contrast to the prevailing, but erroneous, assumption at the time that the mevalonic acid pathway is responsible for the synthesis of isoprenoids in plants.

We now know that the DOXP/MEP pathway is responsible for the biosynthesis of carotenoids, isoprene, mono- and diterpenes, as well as the plant hormones abscisic acid and gibberellins (for isoprene, *see e.g.*, Zeidler *et al*. 1997). Parts of other plant hormones, especially cytokinins, are also made by this pathway. Further, this pathway is also responsible for the synthesis of the side chains of phylloquinone K_1, plastoquinone-9, and the phytol tail of chlorophylls. Hartmut also showed that the DOXP/MEP pathway not only occurs in all photosynthetic organisms (plants, algae, photosynthetic bacteria), but also in pathogenic bacteria and in the malaria parasite *Plasmodium falciparum* (Lichtenthaler 1999, 2000). Based on this information, Hartmut developed a simple test-system to discover new drugs against malaria

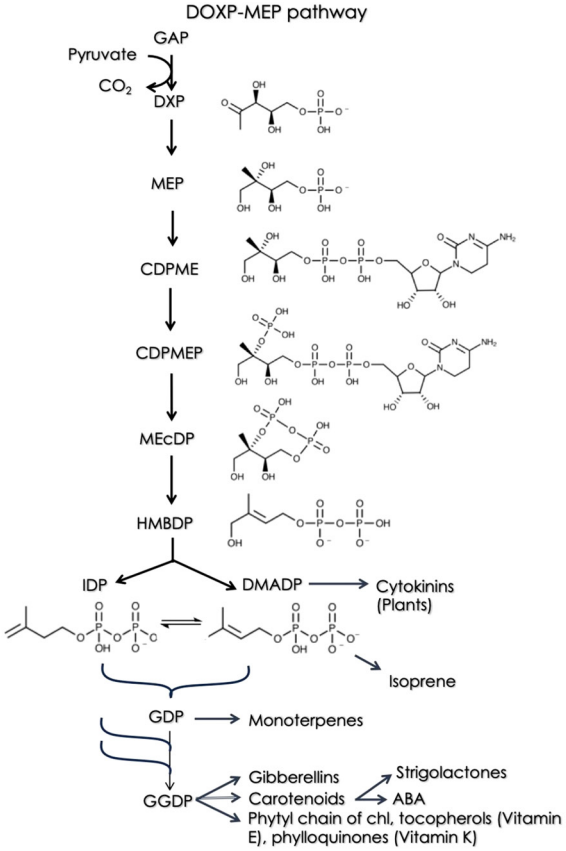

Fig. 2. The DOXP/MEP pathway. This pathway begins with the addition of two carbons from pyruvate to GAP and ends with IDP and DMADP. Many plant growth regulators (hormones) are made by this pathway as well as carotenoids and essential parts of chlorophyll, tocopherols, and phylloquinones. DOXP/MEP – deoxyxylulose-5-phosphate/methylerythritol-4-phosphate, GAP – glyceraldehyde-3-phosphate, DXP – deoxyxylulose-5-phosphate, MEP – methylerythritol-4-phosphate, CDPME – diphosphocytidyl methylerythritol, CDPMEP – diphospho-cytidyl methylerythritol phosphate, MEcDP – methylerythritol cyclodiphosphate, HMBDP – hydroxymethyl butenyl diphosphate, IDP – isopentenyl diphosphate, DMADP – dimethylallyl diphosphate, GDP – geranyl diphosphate, GGDP – geranylgeranyl diphosphate, ABA – abscisic acid.

Fig. 3. A group photograph at a special symposium held at Hartmut's 60th birth anniversary at the University of Karlsruhe on 22 June 1994. *Left to right*: Thomas Bach, Michel Rohmer (both from Strasbourg), Hartmut Lichtenthaler and Peter Biacs (from Budapest, Hungary). *See* text for details.

(Lichtenthaler *et al*. 2000) – a great achievement for human health.

We are indeed delighted to note that Hartmut continues to be active in publishing papers, such as a comprehensive review on his multicolor fluorescence imaging method (Lichtenthaler 2021), and original research papers on the differing values of the ratio of Chl *a*/*b* in C_3 and C_4 plants (Lichtenthaler and Babani 2022), and on the unusual formation of larger leaves with a higher Chl content per leaf area unit in a strongly pruned ginkgo tree (Lichtenthaler *et al*. 2023).

The intellectual environment

A discussion of Hartmut's contributions remains incomplete without mentioning the historical aspects of his association at UC Berkeley – with Melvin Calvin and Andrew (Andy) A. Benson, the co-discoverers of the path of carbon fixation and primary metabolism in photosynthesis (the Calvin–Benson cycle). Hartmut recalls fondly the "Berkeley Spirit" that resulted from young scientists at Berkeley collaborating regardless of which lab they were from. Calvin was especially helpful to young post-docs such as Hartmut. A discussion of Hartmut's personal experiences provides a further fascinating insight into the incredibly productive time in photosynthesis at UC Berkeley in the beginning of 1960s when Daniel Arnon and Melvin Calvin (with their group members) were top leaders in their areas of photosynthesis research. Hartmut Lichtenthaler was uniquely positioned to take advantage of facilities in several laboratories that were making seminal breakthroughs in photosynthesis.

What follows is our distillation of comments from Professor Lichtenthaler (by email) and our own recollection of discussions with him (often by phone). *See* below for more on Melvin Calvin, Dan Arnon, and Andy Benson, as well as on the Berkeley Spirit.

Melvin Calvin: Calvin's photosynthesis research group, known as the Laboratory of Chemical Biodynamics, had its main laboratories in the basement of the Life Sciences Building on the University of California Berkeley campus. There they had Calvin's senior scientist James Alan (Al) Bassham (1922–2012; *see* Govindjee *et al*. 2016), who had obtained his PhD in 1949 working in Calvin's lab. Other members of Calvin's laboratory were Ken Sauer (1931–2022; https://biosciences.lbl.gov/2023/06/01/sauer-leaves-legacy-in-science-and-teaching/), Ning Pon; Roderic (Rod) Park (1932–2013); and Vivian Moses (1928–2017) plus 12 to 15 postdoctoral research fellows, as well as several PhD students. Hartmut Lichtenthaler had started his research in the large laboratory in the Life Sciences Building. He was very much impressed by the excellent equipment with the most modern instruments which, at that time, were not available in Europe, and which opened the possibility for Hartmut to apply and develop novel investigation methods.

These favorable working conditions as well as the continuous personal encouragement by Melvin Calvin

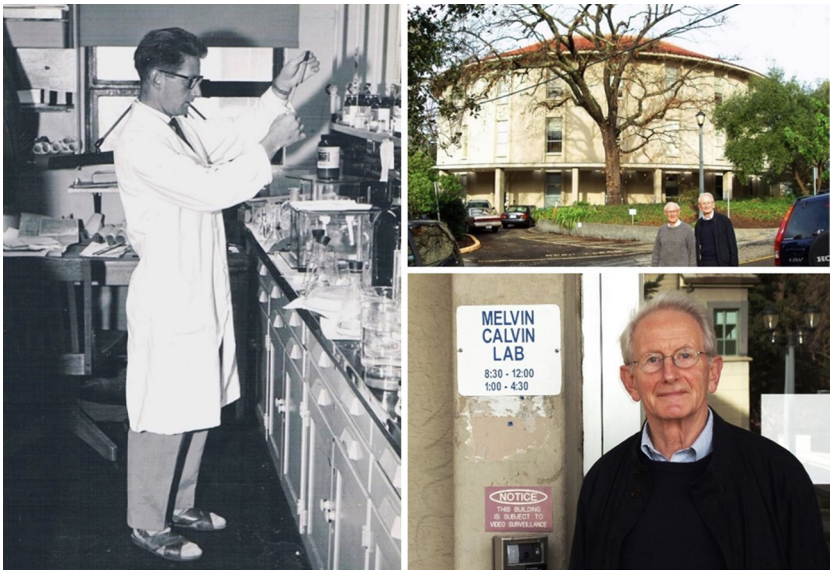

Fig. 4. *Left*: Hartmut Lichtenthaler at his laboratory bench in the summer of 1962, in Melvin Calvin's photosynthesis laboratory, Life Sciences Building, Berkeley. *Top right*: A photograph of the Calvin roundhouse building during Hartmut's 2006 visit; in the foreground are Ken Sauer (1931–2022) and Hartmut. *Bottom right*: Hartmut at the entrance of the Melvin Calvin laboratory, 42 years after he had worked there.

were an essential driving force for the innovative research results by Hartmut [*see* his recollections on Melvin Calvin in Govindjee *et al*. 2020]. Fig. 4 (*left*) shows a 1962 photograph of Hartmut at his lab bench in the Life Sciences Building at UC Berkeley. After Melvin Calvin received, in December 1961, the Nobel Prize for the photosynthetic CO_2 fixation cycle, now known as Calvin–Benson cycle, he was promised his own Laboratory Building on the Berkeley Campus. The groundbreaking ceremony for this new building took place in the early summer of 1962. In September 1963, the newly constructed Roundhouse Building with two laboratory floors, and the radially arranged lab benches, known today as the Melvin Calvin laboratory, was finished and all the group members of the Calvin group moved in. This building is shown in Fig. 4 (*upper right*) during a revisit, in 2006, of Hartmut on the Berkeley Campus. (*See* Fig. 4 (*bottom right*) for an early photo of Hartmut before the door of the "old" Calvin lab.) At this time, Hartmut was reunited with several of his former colleagues, including Rod Park (Fig. 5, *left*) with whom he had earlier published a joint paper in *Nature* on the "Chemical composition of chloroplast lamellae from spinach" (Lichtenthaler and Park 1963). However, Hartmut's major results in the Calvin laboratory dealt with "Quinone and pigment composition of chloroplasts and quantasome aggregates" (Lichtenthaler and Calvin 1964).

Hartmut has told us that working in Calvin's laboratory in the 1960s had proceeded in a very friendly, helpful, and familiar atmosphere, characterized by open interdisciplinary discussions and joint assistance, and that this was not only in research, but also in most personal and social matters. He noted that newcomers to Calvin lab received much assistance by senior scientists and staff members to get started. This was particularly done by Calvin's long-term top technical assistant Martha Kirk. Indeed, there was a great sense of togetherness among the group members; further, there were various joint social activities, such as summer parties in the Tilden Park on the Berkeley Hills (arranged by Melvin Calvin and his wife Genevieve), joint skiing trips to the Sierra Nevada or Mount Shasta, as well as invitation of the group members to Calvin's home. In the fall of 1963, several younger lab members, including Hartmut with his cello, formed a string quartette – playing on Thursdays at lunch time in the seminar room of the Roundhouse to which everybody could attend and listen. In fact, all the Calvin lab associates became members of the large "Calvin family" which also included the former members of the group. When, in 1964, Hartmut returned to Germany *via* Japan, he was invited by the former group member Professor Kazuo Shibata (1917–1983), who is known for the "Shibata shift", a special chemical step in the chlorophyllide and Chl formation process. Here, Hartmut gave a lecture at the Tokyo University. Thereafter, Shibata San (Japanese honorific), showed Hartmut around Tokyo and all its cultural sites. Hartmut returned this hospitality in 1971, after the 2nd International Photosynthesis Congress in Stresa, Italy; he showed Kazuo (and later many other former members of the Calvin's group) his romantic hometown Heidelberg, the medieval castles in the Neckar valley and the Black Forest.

Berkeley, a hotspot for photosynthesis research in the early 1960s: When Hartmut was at UC Berkeley **(**Fig. 4), there were, in addition to Calvin's large group, several others performing essential research in photosynthesis. Chiefly among them was the group of Daniel Arnon (1910–1994; *see* Buchanan 2001), which included Frederick Robert (Bob) Whatley (1924–2020; Govindjee 2022) and Mary Belle Allen (1922–1973; https://en.wikipedia.org/wiki/Mary_Belle_Allen). Arnon, Whatley, and Allen discovered photosynthetic phosphorylation (*see* Arnon *et al*. 1954); Mary Belle Allen had her own laboratory outside the campus. Members of the Arnon group also included Bob Buchanan, Richard Malkin, David Knaff (1941–2016), David Hall (1935–1999; *see* Rao 1999), Shirley Jeffrey (1931–2014) as well as Akira Mitsui (1929–1994). Arnon and Calvin's group members knew each other well and there was good scientific exchange between them. In addition, within the general biochemistry seminars, held in the fall/winter semester in the Biochemistry Building at UC Berkeley, there were a few photosynthesis lectures. This also stimulated the contact and discussion between the postdoctoral fellows of the different photosynthesis research groups of Berkeley. Further, this was enhanced by photosynthesis lectures by leading American and foreign photosynthesis specialists. All this created a very stimulating atmosphere for photosynthesis research in Hartmut's experience.

Daniel Arnon: Daniel (Dan) Arnon was quite interested in Hartmut's findings of phylloquinone K_1, a methyl-phytyl-1,4-naphthoquinone, found to be localized in the photosynthetic biomembrane. Arnon had found that

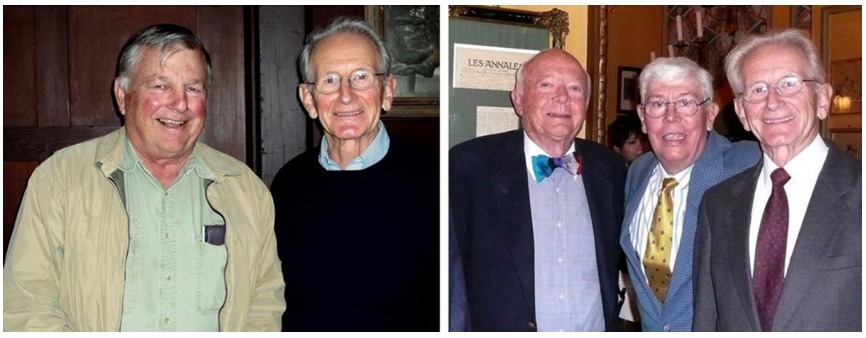

Fig. 5. *Left* (*left to right*): Rod Park (1932–2013) and Hartmut at the Berkeley Faculty Club, in 2006. *Right* (*left to right*): Andy Benson (1917–2015), Roland Douce (1939–2018), and Hartmut Lichtenthaler in the historic restaurant "Le Procope" in Paris, France, during a special dinner, in 2017, for Andy Benson on his 90th birth anniversary.

synthetic naphthoquinones catalyze cyclic photophosphorylation in chloroplasts (for Arnon's research, *see* Buchanan and Tagawa 1995). The two then discussed the possibility for phylloquinone K_1 to be the natural cofactor catalyzing cyclic photophosphorylation. And in 1968, at the 1st International Photosynthesis Congress in Freudenstadt, where Hartmut presented his first evidence that phylloquinone K_1 was indeed specifically bound to Photosystem I (Lichtenthaler 1969), the two then focused on this topic in great depth. Moreover, in the summer of 1973 when Hartmut was a "Visiting Professor" in Calvin's laboratory at Berkeley, Arnon invited him to give a lecture on his newest photosynthesis results. There, and at later meetings, the two discussed various open questions in photosynthesis research.

Andrew Benson: Andy Benson (1917–2015; *see* Buchanan *et al.* 2007, Govindjee 2010, Lichtenthaler *et al.* 2015, Nonomura *et al.* 2017) made the earliest and key contributions to the elucidation of the photosynthetic carbon reduction cycle, known today as the Calvin–Benson cycle, but he worked later on plant lipids, at the La Jolla Campus of the University of California, San Diego. Andy retained close contact with members of Melvin Calvin's group, even though he had left the group in 1956! Benson is also well-known for his interest in the arrangement of the different glycerolipids in the photosynthetic membrane. When Hartmut's paper on the chloroplast lipids (pigments, quinones, and glycerolipids) was published in the summer of 1963 (Lichtenthaler and Park 1963), Benson invited him to deliver a seminar on this research. This visit and discussion between Hartmut and Andy Benson in October 1963 was the beginning of their lifelong friendship. Forty-four years later, Hartmut Lichtenthaler, together with Bob Buchanan and Roland Douce (1939–2018), edited a special issue of *Photosynthesis Research* with 18 papers dedicated to Andy Benson on the occasion of his 90th birthday anniversary (Buchanan *et al.* 2007). This special issue was presented during a dinner, hosted by the three to Andy Benson and his wife Dee, in the historical restaurant "Le Procope" in Paris, France (Lichtenthaler *et al.* 2008); *see* Fig. 5 (*right*). It is of particular interest in this context that all the four, mentioned here, and one of the authors (GG) had been recipients of the Rebeiz Foundation Lifetime Achievement Award for their groundbreaking innovative photosynthesis research: Govindjee in 2007; Andy Benson in 2009; Bob Buchanan in 2012; Roland Douce in 2014; and Hartmut Lichtenthaler in 2015 (*see* Rebeiz *et al.* 2007, Lichtenthaler 2020).

Thus, in the early 1960s, UC Berkeley was a very stimulating hotspot for photosynthesis research and created for young researchers an atmosphere of inspiration and enlightenment that Hartmut benefited from and later termed it the "Berkeley Spirit." This was included in the obituary of Shirley Jeffrey, a marine biologist, who, like him, was a postdoc at the University of California Berkeley from 1962 to 1964: "We all were enlightened by the then great "Berkeley Spirit" to dedicate our life to science and to try to make basic, essential, and innovative contributions. It was an atmosphere of departure! And this "Berkeley Spirit" kept us busy in science over the last five decades" (for full text, *see* Appendix 1 and Wright *et al.* 2015).

A lecture by Lichtenthaler on Joseph Kölreuter

On 5 October 2023 at the renaming of the Botanical Institute of Karlsruhe to Joseph Gottlieb Kölreuter Institute of Plant Science, JIKP, Hartmut Lichtenthaler gave the historical introductory lecture "Karlsruhe Botany and Joseph Kölreuter (1733–1806)" (*see* Karlsruhe Botany and J.G. Kölreuter, the founder of genetics). Fig. 6 shows Hartmut with the current faculty members of the institute.

Service, honors, awards, and recognition

Hartmut Lichtenthaler and his international connections: Hartmut was an active participant in the first International Photosynthesis Congress (IPC) held from 4 to 8 June 1968 in Freudenstadt, Black Forest, Germany, initiated and organized by Helmut Metzner (1925–1999), Tübingen, who was also a former member of Calvin's group at Berkeley. This was the first international meeting on photosynthesis after World War II, where scientists, from both the East and West, came together to discuss and exchange their recent results on photosynthesis. All the leading photosynthesis researchers were present, including Alexander A. Krasnovsky (1913–1993; for Krasnovsky, *see* Karapetyan and Govindjee 2014) from Moscow (Russia), Melvin Calvin (1911–1997), and Daniel Arnon (1910–1994) both from UC Berkeley, and Trevor Goodwin (1916–2008), from Wales, as well as many

Fig. 6. *Left to right*: Professors Tilman Lamparter, Peter Nick, Hartmut Lichtenthaler (Emeritus), Natalia Requena, and Holger Puchta (Head of the Department). Place: Joseph Gottlieb Kölreuter Institute of Plant Sciences (JKIP); date: 5 October 2023.

young scientists then including one of us (Govindjee). In addition, Zdeněk Šesták (1932–2008) from the Czech Academy of Sciences in Prague was also there, who in 1967 founded the journal *Photosynthetica*, in which authors from the East and West could publish their research findings (*see* Govindjee *et al*. 2002, Lichtenthaler 2018).

Hartmut reminded us recently that Melvin Calvin himself was there together with two members of his research group: James Al Bassham (1922–2012) and Kenneth Sauer (1931–2022). In addition, 13 former members of Calvin's group participated, seven from Germany, three from France, and a few from other countries. And on one evening scientists of the "Calvin family" had a grand reunion together with Melvin Calvin at a Freudenstadt restaurant.

In addition to the above-mentioned first photosynthesis congress (for history and photographs, *see* Govindjee and Yoo 2007), Hartmut was a participant in all the subsequent congresses, up to 1998. In the 3rd International Photosynthesis Congress, organized by Mordhay Avron (1931–1991), in 1974, at the Weizmann Institute of Sciences, in Rehovot, Israel, Hartmut participated with four members of his Karlsruhe research group (Fig. 7). The 5th Photosynthesis Congress, held in 1980 in Halkidiki, Greece, was organized by the late George Akoyunoglou (1927–1986), a former PhD student of Melvin Calvin. Further, the 7th International Photosynthesis Congress, held in 1986, in Providence, Rhode Island, was organized by John Biggins (1936–2004), who had earlier received his PhD under the guidance of Rod Park and Melvin Calvin.

Hartmut, Zdeněk Šesták, the journal *Photosynthetica*, and the Czech Republic: It was at the 1st International Congress of Photosynthesis in 1968 in Freudenstadt, Germany, that Hartmut first met Zdeněk Šesták (1932–2008), who, in 1967, had started, on behalf of the Czech Academy of Sciences, to edit *Photosynthetica*, a new international journal (*see* Lichtenthaler 2018). There, the two discussed key aspects of the then current and the future research in photosynthesis. This was the beginning of a lifelong friendship. In the following years, they met several times at various photosynthesis meetings in Germany and in other European countries. Hartmut visited the laboratories of the Czech Academy of Sciences in Prague and delivered lectures on his research. In addition, Hartmut invited Šesták, Jiří Čatský, and other members of the Czech Academy of Sciences for seminars in Karlsruhe. Moreover, with the financial support of a German foundation, Hartmut invited Šesták as well as Pavel Šiffel to the 1988 International Chlorophyll Fluorescence Symposium in Bad Honnef, Germany, giving them an opportunity to present their research to the international community.

Following the collapse of the "Iron Curtain" and the dissolution of the Soviet Union in November 1989, Šesták was able to include western scientists on the editorial board of *Photosynthetica.* Hartmut was invited to become a board member and served in this capacity until 2005. In addition, he published much of his research in *Photosynthetica*, which included a wonderful historical review of the Kautsky effect "60 years of chlorophyll fluorescence induction kinetics" (Lichtenthaler 1992). Further collaboration of Hartmut with the Czech Republic included invitations to young scientists, Jiří Šantrůček and Pavel Šiffel, from České Budějovice for a research stay in Karlsruhe (*see* Šantrůček *et al*. 1992, Šiffel *et al.* 1993). In addition, Hartmut organized a one-year-stay for Roman Hák (from Lubomir Nátr's group of the Charles University of Prague) as a postdoctoral fellow in his laboratory in Karlsruhe (*see* Hák *et al.* 1993). In 2003, Hartmut Lichtenthaler was honored by the Czech Academy of Sciences in Prague through award of the Gregor Mendel Honorary Medal for Merits in Bio-Sciences. It was Zdeněk Šesták who delivered the laudatory speech on this occasion (*see* Lichtenthaler 2018).

Hartmut has also kept close scientific contacts and cooperation with scientists from several Czech universities: Stanislav Procházka (from the Mendel University, Brno), Michal Marek and Otmar Urban (from the Institute of Systems Biology and Ecology of the Czech Academy of Sciences in Brno; *see* Lichtenthaler *et al*. 2007b for one of their joint publications). Further, in 2017, Hartmut delivered the laudatory speech at the 50th anniversary of *Photosynthetica* (Lichtenthaler 2018). Fig. 8 shows his

Fig. 7. A 1974 group photograph at the 3rd International Photosynthesis Congress, Rehovot, Israel. *Left to right*: Claus Buschmann, Hartmut Lichtenthaler, Karl Grumbach, Klaus Pfister, and Hans Kleudgen (Note: Claus, Karl, Klaus, and Hans were members of Hartmut's research group in Germany).

Fig. 8. A 2017 photograph at the Czech Academy of Sciences, Prague. *From left to right*: Hartmut Lichtenthaler, Jana Pospíšilová, and Győző Garab at the celebration of the 50th anniversary of *Photosynthetica.*

photograph with Jana Pospíšilová and Győző Garab, two other members of the editorial board of *Photosynthetica*.

Promotion of European plant physiologists: Hartmut is one of the founding fathers of the Federation of European Societies of Plant Physiology (FESPP) established in 1978 and has served as its President during 1984–1986 and then as its Past-President from 1986 to 1988. In 1986, Hartmut organized the 5th FESPP Congress in Hamburg, Germany. Fig. 9 shows Hartmut as the President of this Congress, at its opening ceremony. During his presidency, he managed the FESPP affairs and expanded membership quite well – despite the initial reluctance from some East European communist authorities. Thanks to his persistent efforts, East European plant physiologists from Russia, Hungary, the Czech Republic, and East Germany were able to become members of the European Federation (FESPP) and could thus participate in 1988 in the 6th FESPP Congress in Split, Yugoslavia (*see* Lichtenthaler 2004a).

Historical reporter: Hartmut Lichtenthaler has described wonderfully well the history and the development of co-operation and the international symposia series, such as the FESPP (Lichtenthaler 2004a), as well as that of the International Symposia on Plant Lipids, the ISPLs, being held every two years, which he had organized in 1976, in Karlsruhe, and transformed them to international meetings (Lichtenthaler 2004b). In addition, Hartmut has also authored several obituaries/tributes, or historical notes on Andy Benson (Lichtenthaler *et al.* 2015), Roland Douce (Joyard and Lichtenthaler 2019), Melvin Calvin (Govindjee *et al.* 2020), and Zdeněk Šesták (Lichtenthaler 2018). In addition, he has written an article on Govindjee, one of the authors of the current article (*see* Lichtenthaler 2020).

We emphasize that Hartmut has been a great scientific coordinator as well as a topmost organizer of many scientific meetings and symposia (*see* Appendix 2 for a chronological list).

Promotion of junior scientists: Hartmut Lichtenthaler has always been very active in the promotion of young

Fig. 9. *Top*: A photograph at the opening ceremony of the 5th FESPP congress in Hamburg, held in August 1986. *Left to right*: Cornelius Karssen (Treasurer), Peter Böger (Secretary General), and Hartmut Lichtenthaler (President). *Bottom*: A photograph of Hartmut Lichtenthaler (in the center of the photo) at the 5th FESPP congress in Hamburg during a reception at the University of Hamburg. On the right of Hartmut is Itzhak Ohad (1930–2016) from Israel, and then Raphael Goren, also from Israel; on the extreme right is Pedro J. Aparicio of Spain, all three were chairmen of the FESPP congress.

scientists. Together with his colleagues from other German universities, he organized yearly workshops for PhD students and young plant scientists where they could present and discuss their research results. In 1980, he initiated in Karlsruhe the yearly "Photosynthesis Workshops" for PhD students and young researchers of six South-German universities (in Darmstadt, Frankfurt, Freiburg, Kaiserslautern, Karlsruhe, and Konstanz), a series that was held until 2004, with five meetings in Karlsruhe (*see* Photosynthesis Workshops). Hartmut has also participated, with his juniors, in the annual "Rhein-Main Botany Colloquia" series of ten German universities (*see* Lichtenthaler 2004a,b), two of which he organized in 1989 and 1997 in Karlsruhe.

Hartmut and books: Hartmut has authored two books: (*1*) "Practical Course of Photosynthesis" (in German), Quelle & Meyer Verlag, Heidelberg, 1978; and (*2*) "The Forest Decline in a Botanical View" (in German), G. Braun Verlag, Karlsruhe, 1984. In addition, he has edited four books: (*1*) "Lipids and Lipid Polymers in Higher

Plants", Springer Verlag, Berlin, 1977 (with M. Tevini); (*2*) "Applications of Chlorophyll Fluorescence", Kluwer Academic Publishers, Dordrecht, 1988; (*3*) "Vegetation Stress", G. Fischer Verlag, Stuttgart, 1996; and (*4*) "The Chloroplast: Basics and Applications", Springer, Dordrecht, The Netherlands, 2010 (with C.A. Rebeiz and others).

Hartmut Lichtenthaler, a highly cited author in plant biology: On a world-wide level, Hartmut is one of the most cited authors in photosynthesis, plant physiology, and plant biochemistry. He has a long career of more than 65 years in scientific research – starting with his PhD thesis in the fall of 1958. According to *Research Gate* (February 2024) his 486 research papers, published from 1962 to 2023, reached 46,000 citations and 110,000 reads. His h-index is 81. *Google Scholar* lists him in February 2024 with 57,000 citations and an h-index of 84.

Honors: In recognition of his outstanding scientific achievements, his continuous promotion of international scientific cooperation and exchange, and his efforts to institute and establish the European Federation of Plant Physiology, Hartmut Lichtenthaler has been honored with multiple awards including three honorary doctorates (Dr.h.c.) from (*1*) the Mendel University of Brno, the Czech Republic (1996); (*2*) Eötvös Loránd University, Budapest (1997); and (*3*) the Szent István University, Gödöllö, Hungary (2001). In addition, in 2001, he has received the prestigious "Cross of Merits of the Federal Republic of Germany" (Bundesverdienstkreuz am Bande). Further, in 2010, Hartmut received the "Corresponding Membership Award of the American Society of Plant Biologists", ASPB, accentuating his recognition in the worldwide community of plant physiologists. In 2015, Hartmut was honored with the prestigious "Lifetime Achievement Award (LTA-Award) for Photosynthesis" of the Rebeiz Foundation, in Champaign, Illinois, USA, for his "groundbreaking discoveries in chloroplast structure and isoprenoid biochemistry" (*see* Fig. 10). Last but not the least, in 2017, he became an Honorary Member of the German Botanical Society (DBG).

Hartmut Lichtenthaler as a dynamic scientist: In one of the testimonials read, when in 2015 Hartmut received the Lifetime Achievement Award of the Rebeiz Foundation, Prof. Thomas Bach from the University of Strasbourg, France, his former PhD student, wrote: "Hartmut's lectures were indeed fascinating, filled with news on latest research in photosynthesis. He has set a high standard in the organization of international collaboration and projects across borders, at a time when the "Iron Curtain" was still existing, as well as an editor of books and as author of an impressive number of articles. And he is still maintaining his deep interest in photosynthesis research. – Hartmut really drove his group with his dynamics and "speed", with his hunger for new data. The door to his office was usually kept open. He also gained a special reputation for his dynamic attitude at the University of Karlsruhe". Further, in 1994 the University of Karlsruhe celebrated Hartmut's 60th birthday with a special "Lichtenthaler Symposium".

A special message from one of the authors (Anastasios Melis)

We give the last word on Hartmut's science by one of us; Tasso Melis writes: "My associates and I benefited from Hartmut Lichtenthaler's pivotal research on the DOXP/MEP isoprenoid biosynthetic pathway in chloroplasts. His work provided the impetus and guiding principle on converting cyanobacteria to cell factories for heterologous isoprene and, subsequently, ß-phellandrene production. Further, his in-depth description of chloroplast structural acclimation to growth irradiance (sun-type *vs*. shade-type chloroplasts) comprising intricate differences and adjustments in ultra-structure and thylakoid arrangements played an important supporting role for my research at a critical time when the question of photosystem stoichiometry adjustments and optimization in chloroplasts was being heavily debated. Aside from photosynthesis, I still fondly remember the time, during a break from the International Symposium on "Applications of Chlorophyll Fluorescence" in Bad Honnef, when Hartmut took us on a long walk through the Rhine valley vineyards up to the Drachenfels castle. All these have left indelible positive memories, indeed."

Fig. 10. A 2015 photograph at the Rebeiz Foundation, of Champaign, Illinois, USA, when Hartmut Lichtenthaler received the Lifetime Achievement Award for Excellence in Photosynthesis. *Left to right*: Govindjee, William (Bill) Cramer, Hartmut Lichtenthaler, Bruce Diner, Pierre Joliot, Tino Rebeiz, and Thomas D. (Tom) Sharkey.

Fig. 11. *Top*: A 2005 photograph of Hartmut Lichtenthaler (in the middle) with his wife Regine (on his left) and son Stefan (on his right), who is a professor of Medical Biochemistry in Munich, while they were on a hiking trip in the Alps at the Lech-Arlberg Pass. *Bottom*: Alpine flowers in Tirol photographed by Hartmut Lichtenthaler. On the left is Lady's slipper orchid at 2,000 m in 2018 and on the right is the blue Clusius's gentian at 1,650 m in 2023; photographs provided by Hartmut Lichtenthaler.

Hartmut, a friend of Alpine Mountains

As many friends of Hartmut have told us, he indeed has a great passion to hike in the high mountain regions of the European Alps, in Austria, France, Germany, Italy, and Switzerland, and to search and explore the local alpine flowers, orchids, and gentians at their natural alpine habitats, a passion shared by his family (Fig. 11). In his formative years, Hartmut also climbed various mountain peaks and was a very passionate skiing fellow. He started this activity already in the summer of 1961, when he was working as a research fellow at the Centre d'Ètudes Nucléaires de Grenoble, France.

With the alpine club there he would hike on the weekends and would climb several mountain tops of the Dauphiné Alps (*e.g.*, the Meije, 3,983 m). Later, during his stay in Berkeley, California, from 1962 to 1964, Hartmut was known to hike on weekends through the High Sierra Nevada mountains following the John Muir Trail. During this period, he climbed the Half Dome in the Yosemite National Park, was at the summit of Mount Whitney (4,421 m), and also Mount Shasta (4,322 m). In 1964, on his return trip to Germany, he made a stopover in Java, Indonesia, to visit the famous Botanical Garden of Bogor and the alpine gardens of Tjibodas, and climbed there with several Indonesian friends the two peaks of the active volcano mountain Gede (2,958 m and 3,019 m). Finally in 1992, after the 9th International Photosynthesis Congress held in Nagoya, Japan, he hiked to the top of Mount Fuji (3,776 m) with a younger Japanese colleague; Hartmut was 58 years old at the time!

Concluding remarks

Hartmut Lichtenthaler has devoted his life to science, research, teaching, and international cooperation with passion (*see* Lichtenthaler 2015). He is a dedicated, charismatic scientist and a great plant biochemist. He is a very active and highly dedicated person, who has advanced not only photosynthesis and plant science research, but also international scientific communication and cooperation, as well as the promotion of young scientists. With his curiosity for the world of nature, his broad knowledge, and commitments, he has inspired students and colleagues around the world. Hartmut is a sportive and broadly educated person with an enormous knowledge not only in science, but also in the history and the arts. It is always a pleasure to talk with him and to be his friend.

On behalf of his friends and colleagues throughout the world of science, we congratulate you, Hartmut, Professor Emeritus Hartmut Karl Lichtenthaler, on your 90th birthday and extend warm wishes for the future – in this special issue of *Photosynthetica* – honoring you and your brilliant academic life.

References

Arnon D.I., Whatley F.R., Allen M.B.: Photosynthesis by isolated chloroplasts. II. Photosynthetic phosphorylation, the conversion of light into phosphate bond energy. – J. Am. Chem. Soc. **76**: 6324-6329, 1954.

Blankenship R.E.: Molecular Mechanisms of Photosynthesis. 3rd Edition. Pp. 352. John Wiley & Sons, Hoboken 2021.

Buchanan B.B.: Daniel I. Arnon (1910-1994). – In: Biographical Memoirs of the National Academy of Sciences. Vol. 80. Pp. 20. The National Academy Press, Washington 2001.

Buchanan B.B., Douce R., Lichtenthaler H.K.: Andrew A. Benson. – Photosynth. Res. **92**: 143-144, 2007.

Buchanan B.B., Tagawa K.: Perspective on Daniel I. Arnon's contributions to research, 1960–1994. – Photosynth. Res. **46**: 27-35, 1995.

Buschmann C., Lichtenthaler H.K.: Principles and characteristics of multi-colour fluorescence imaging of plants. – J. Plant Physiol. **152**: 297-314, 1998.

Golz A., Focke M., Lichtenthaler H.K.: Inhibitors of *de novo* fatty acid biosynthesis in higher plants. – Plant Physiol. **143**: 426-433, 1994.

Govindjee G.: Celebrating Andrew Alm Benson's 93rd birthday. – Photosynth. Res. **105**: 201-208, 2010.

Govindjee G.: Frederick Robert (Bob) Whatley (1924-2020): Co-discoverer of photophosphorylation in chloroplasts and much more. – J. Plant Sci. Res. **38**: 1-7, 2022.

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

Govindjee G., Nonomura A., Lichtenthaler H.K.: Remembering Melvin Calvin (1911-1997), a highly versatile scientist of the 20th century. – Photosynth. Res. **143**: 1-11, 2020.

Govindjee G., Šesták Z., Peters W.R.: The early history of "Photosynthetica", "Photosynthesis Research" and their publishers. – Photosynthetica **40**: 1-11, 2002.

Govindjee G., Yoo H.: The International Society of Photosynthesis research (ISPR) and its associated International Congress on Photosynthesis (ICP): a pictorial report. – Photosynth. Res. **91**: 95-106, 2007.

Hák R., Rinderle-Zimmer U., Lichtenthaler H.K., Nátr L.: Chlorophyll *a* fluorescence signatures of nitrogen-deficient barley leaves. – Photosynthetica **28**: 151-159, 1993.

Hu K., Govindjee G., Tan J. *et al.*: Co-author and co-cited reference network analysis for chlorophyll fluorescence research from 1991 to 2018. – Photosynthetica **58**: 110-124, 2020.

Interschick-Niebler E., Lichtenthaler H.K.: Partition of phylloquinone K_1 between digitonin particles and chlorophyll-proteins of chloroplast membranes from *Nicotiana tabacum*. – Z. Naturforsch. C **36**: 276-283, 1981.

Joyard J., Lichtenthaler H.K.: Tribute: Roland Douce, 1939–2018. – Photosynth. Res. **141**: 131-142, 2019.

Karapetyan N.V., Govindjee G.: Alexander Abramovich Krasnovsky (1913-1993): 100th birth anniversary in Moscow, Russia. – Photosynth. Res. **120**: 347-353, 2014.

Kobek K., Focke M., Lichtenthaler H.K. *et al.*: Inhibition of fatty acid biosynthesis in isolated chloroplasts by cycloxydim and other cyclohexane-1,3-diones. – Physiol. Plantarum **72**: 492-498, 1988.

Lichtenthaler H.K.: Plastoglobuli and the fine structure of plastids. – Endeavour **XXVII**: 144-149, 1968.

Lichtenthaler H.K.: Localization and functional concentrations of lipoquinones in chloroplasts. – In: Metzner H. (ed.): Progress in Photosynthesis Research. Proceedings of First International Congress of Photosynthesis Research, held at Freudenstadt 1968. Vol 1. Pp. 304-314. H. Laupp, Tübingen 1969.

Lichtenthaler H.K.: Chlorophylls and carotenoids, the pigments of photosynthetic biomembranes. – Method. Enzymol. **148**: 350-382, 1987.

Lichtenthaler H.K.: *In vivo* chlorophyll fluorescence as a tool for stress detection on plants. – In: Lichtenthaler H.K. (ed.): Applications of Chlorophyll Fluorescence in Photosynthesis Research, Stress Physiology and Remote Sensing. Pp. 129-142. Springer, Dordrecht 1988.

Lichtenthaler H.K.: Mode of action of herbicides affecting acetyl-CoA carboxylase and fatty acid biosynthesis. – Z. Naturforsch. C **45**: 521-528, 1990.

Lichtenthaler H.K.: The Kautsky effect: 60 years of chlorophyll fluorescence induction kinetics. – Photosynthetica **27**: 45-55, 1992.

Lichtenthaler H.K.: The 1-deoxy-D-xylulose-5-phosphate pathway of isoprenoid biosynthesis in plants. – Annu. Rev. Plant Biol. **50**: 47-65, 1999.

Lichtenthaler H.K.: Non-mevalonate isoprenoid biosynthesis: enzymes, genes and inhibitors. – Biochem. Soc. T. **28**: 785-789, 2000.

Lichtenthaler H.K.: A history of the Federation of European Societies of Plant Physiology FESPP since its formation in 1978 – including notes on events preceding the foundation and following re-naming as the Federation of European Societies of Plant Biology (FESPB) in 2002. – J. Plant Physiol. **161**: 635-639, 2004a.

Lichtenthaler H.K.: Thirty years of international symposia of plant lipids. – In: Biacs P., Gerely P. (ed.): Proceedings of the 16th Plant Lipid Symposium. Pp. I-XXXI. Méte, Budapest 2004b.

Lichtenthaler H.K.: Biosynthesis, accumulation and emission of carotenoids, α-tocopherol, plastoquinone and isoprene in leaves under high photosynthetic irradiance. – Photosynth. Res. **92**: 163-179, 2007.

Lichtenthaler H.K.: Plastoglobuli, thylakoids, chloroplast structure and development of plastids. – In: Biswal B., Krupinska K., Biswal U.C. (ed.): Plastid Development in Leaves during Growth and Senescence. Advances in Photosynthesis and Respiration. Vol. 36. Pp. 337-361. Springer, Dordrecht 2013.

Lichtenthaler H.K.: Fifty-five years of research on photosynthesis, chloroplasts, and stress physiology of plants: 1958–2013. – In: Lüttge U., Beyschlag W. (ed.): Progress in Botany. Vol. 76. Pp. 3-42. Springer, Cham 2015.

Lichtenthaler H.K.: Zdeněk Šesták and Photosynthetica, a tribute. – Photosynthetica **56**: 1-6, 2018.

Lichtenthaler H.K.: My contact and cooperation with Govindjee over the last five decades: Chlorophyll fluorescence and Rebeiz Foundation. – Photosynthetica **58**: 976-983, 2020.

Lichtenthaler H.K.: Multi-colour fluorescence imaging of photosynthetic activity and plant stress. – Photosynthetica **59**: 364-380, 2021.

Lichtenthaler H.K., Abuslima E., Nick P.: Strong increase of photosynthetic pigments and leaf size in a pruned *Ginkgo biloba* tree. – Photosynthetica **61**: 297-307, 2023.

Lichtenthaler H.K., Ač A., Marek M.V. *et al.*: Differences in pigment composition, photosynthetic rates and chlorophyll fluorescence images of sun and shade leaves of four tree species. – Plant Physiol. Biochem. **45**: 577-588, 2007b.

Lichtenthaler H.K., Babani F.: Detection of photosynthetic activity and water stress by imaging the red chlorophyll fluorescence. – Plant Physiol. Biochem. **38**: 889-895, 2000.

Lichtenthaler H.K., Babani F.: Light adaptation and senescence of the photosynthetic apparatus: changes in pigment composition, chlorophyll fluorescence parameters and photosynthetic activity. – In: Papageorgiou G., Govindjee G. (ed.): Chlorophyll Fluorescence: A Signature of Photosynthesis. Pp. 713-736. Springer, Dordrecht 2004.

Lichtenthaler H.K., Babani F.: Level of photosynthetic pigments and ratios of chlorophyll *a*/*b* and chlorophylls to carotenoids $(a+b)/(x+c)$ in C_4 plants as compared to C_3 plants. – Photosynthetica **60**: 3-9, 2022.

Lichtenthaler H.K., Babani F., Langsdorf G.: Chlorophyll fluorescence imaging of photosynthetic activity in sun and shade leaves of trees. – Photosynth. Res. **93**: 235-241, 2007a.

Lichtenthaler H.K., Buchanan B.B., Douce R.: Honoring Andrew Benson in Paris: A tribute on his 90th birthday. – Photosynth. Res. **96**: 181-183, 2008.

Lichtenthaler H.K., Buchanan B.B., Douce R., Govindjee G.: Andrew A. Benson, 1917–2015. – Photosynth. Res. **124**: 131-135, 2015.

Lichtenthaler H.K., Burkard G., Grumbach K.H., Meier D.: Physiological effects of photosystem II-herbicides on the development of the photosynthetic apparatus. – Photosynth. Res. **1**: 29-43, 1980.

Lichtenthaler H.K., Buschmann C., Döll M. *et al.*: Photosynthetic activity, chloroplast ultrastructure, and leaf characteristics of high-light and low-light plants and of sun and shade leaves. – Photosynth. Res. **2**: 115-141, 1981.

Lichtenthaler H.K., Buschmann C.: Das Baumsterben aus botanischer Sicht. [Forest Decline in a Botanical View]. Pp. 87. G. Braun Verlag, Karlsruhe 1984a. [In German]

Lichtenthaler H.K., Buschmann C.: Photooxidative changes in pigment composition and photosynthetic activity of air-polluted spruce needles (*Picea abies* L.). – In: Sybesma C. (ed.): Advances in Photosynthesis Research. Advances in Agricultural Biotechnology. Vol. 4. Pp. 245-250. Springer, Dordrecht 1984b.

Lichtenthaler H.K., Buschmann C.: Chlorophylls and carotenoids: Measurement and characterization by UV-VIS spectroscopy. – In: Current Protocols in Food Analytical Chemistry. Suppl. 1. Pp. F4.3.1-F4.3.8. John Wiley & Sons, New York 2001.

Lichtenthaler H.K., Calvin M.: Quinone and pigment composition of chloroplasts and quantasome aggregates from *Spinacia oleracea*. – BBA-Biophys. Subj. **79**: 30-40, 1964.

Lichtenthaler H.K., Kuhn G., Prenzel U. *et al.*: Adaptation of chloroplast-ultrastructure and of chlorophyll-protein levels to high-light and low-light growth conditions. – Z. Naturforsch. C **37**: 464-475, 1982.

Lichtenthaler H.K., Langsdorf G., Buschmann C.: Uptake of diuron and concomitant loss of photosynthetic activity in leaves as visualized by imaging the red chlorophyll fluorescence. – Photosynth. Res. **116**: 355-361, 2013.

Lichtenthaler H.K., Park R.B.: Chemical composition of chloroplast lamellae from spinach. – Nature **198**: 1070-1072, 1963.

Lichtenthaler H.K., Rinderle U.: The role of chlorophyll fluorescence in the detection of stress conditions in plants. – CRC Crit. Rev. Anal. Chem. **19**: S29-S85, 1988a.

Lichtenthaler H.K., Rinderle U.: Chlorophyll fluorescence signatures as vitality indicator in forest decline research. – In: Lichtenthaler H.K. (ed.): Applications of Chlorophyll Fluorescence in Photosynthesis Research, Stress Physiology, Hydrobiology and Remote Sensing. Pp. 143-149. Springer, Dordrecht 1988b.

Lichtenthaler H.K., Schwender J., Disch A., Rohmer M.: Biosynthesis of isoprenoids in higher plant chloroplasts proceeds via a mevalonate-independent pathway. – FEBS Lett. **400**: 271-274, 1997.

Lichtenthaler H.K., Zeidler J., Schwender J., Müller C.: The non-mevalonate isoprenoid biosynthesis of plants as a test-system for new herbicides and drugs against pathogenic bacteria and the malaria parasite. – Z. Naturforsch. C **55**: 305-313, 2000.

Nonomura A.M., Holtz B., Biel K.Y. *et al.*: The paths of Andrew A. Benson: a radio-autobiography. – Photosynth. Res. **134**: 93-105, 2017.

Pfister K., Buschmann C., Lichtenthaler H.K.: Inhibition of the photosynthetic electron transport by bentazone. – In: Proceedings of the Third International Congress on Photosynthesis. Vol. 1. Pp. 675-681. Elsevier, New York 1975.

Rao K.K.: Obituary of David Hall (1935-1999). – Photosynth. Res. **62**: 117-119, 1999.

Rebeiz C.A., Benning C., Bohnert H. *et al.*: Govindjee was honored with the First Lifetime Achievement Award, and Britta Förster and coworkers, with the First Annual Paper Prize of the Rebeiz Foundation for Basic Research. – Photosynth. Res. **94**: 147-151, 2007.

Rinderle U., Lichtenthaler H.K.: The various chlorophyll fluorescence signatures as a basis for physiological ground truth control in remote sensing of forest decline. – In: 12th Canadian Symposium on Remote Sensing Geoscience and Remote Sensing, Vancouver, BC, Canada. Vol. 2. Pp. 674-677. IEEE, Vancouver 1989.

Rock B.N., Hoshizaki T., Lichtenthaler H.K., Schmuck G.: Comparison of *in situ* spectral measurements of forest decline symptoms in Vermont (U.S.A.) and the Schwarzwald (F.R.G.). – In: Proceedings of the International Geoscience and Remote Sensing Symposium, 1986, Zürich. Vol. 3. Pp. 1667-1672. ESA Publications Division, Noordwijk 1986.

Šantrůček J., Šiffel P., Lang M. *et al.*: Photosynthetic activity and chlorophyll fluorescence parameters in *aurea* and green forms of *Nicotiana tabacum*. – Photosynthetica **27**: 529-543, 1992.

Seybold A., Egle K.: Lichtfeld und Blattfarbstoffe I. [Light field and leaf pigments I.] – Planta **26**: 491-496, 1937. [In German]

Sharkey T.D., Govindjee G.: Hartmut Lichtenthaler: an authority on chloroplast structure and isoprenoid biochemistry. – Photosynth. Res. **128**: 117-123, 2016.

Šiffel P., Šantrůček J., Lang M. *et al.*: Age dependence of photosynthetic activity, chlorophyll fluorescence parameters and chloroplast ultrastructure in *aurea* and green forms of *Nicotiana tabacum Su*/*su* mutant. – Photosynthetica **29**: 81-94, 1993.

Stirbet A., Lazár D., Guo Y., Govindjee G.: Photosynthesis: basics, history and modelling. – Ann. Bot.-London **126**: 511-537, 2020.

Wright S.W., Hallegraeff G.M., Mantoura R.F.C.: Shirley W. Jeffrey, 1930-2014. – In: Biographical Memoirs. Pp. 18. National Academy of Sciences, 2015.

Zeidler J.G., Lichtenthaler H.K., May H.U., Lichtenthaler F.W.: Is isoprene emitted by plants synthesized via the novel isopentenyl pyrophosphate pathway? – Z. Naturforsch. C **52**: 15-23, 1997.

Appendix 1. Hartmut Lichtenthaler on the "Berkeley Spirit" in the 1960s stimulating young scientists

"Our joint time more than fifty years ago in Berkeley together with other young postdocs was a wonderful time in our lives. In the early 1960s, the scientific world was wide open for us. With new methods of investigation, advanced scientific instruments, and new chromatographic techniques (*e.g.*, radiolabeling of cellular metabolites, electron microscopy, sensitive recording two-wavelength spectrophotometers, [and] TLC), one could start almost in any field and make large scientific progress. We all were enlightened by the then great "Berkeley Spirit" to dedicate our life to science and to try to make basic, essential, and innovative contributions. It was an atmosphere of departure! And this "Berkeley Spirit" kept us motivated and busy in science over the next five decades. It was a lifelong commitment for Shirley and me and many others who were postdocs in Berkeley at that time. All of us coming from different "nations" felt then that we were belonging to a worldwide international science family. And this knowledge led to life-long personal contacts and to a continuous international scientific cooperation that was the essential basis of the large progress made in plant science and marine biology during the past half century."

Appendix 2. Scientific meeting leadership

Hartmut Lichtenthaler has been an organizer of many scientific meetings since he is convinced that progress in photosynthesis and plant science could only be achieved by exchange of scientific results and ideas as well as joint research endeavours. A few examples of his active participation are shown below.

Year(s)	Name of the conference/program	Place and more	Comment
1976	2nd International Symposium on Plant Lipids: "Lipids and Lipid-Polymers in Higher Plants"	University of Karlsruhe, Germany	*See*: Lichtenthaler 2004b, http://www.ispl2012.org/documents/ISPL_History.pdf.
1981	International Symposium: "Photosynthesis and Biological Solar Energy Conversion"	October 11–14, 1981, Ettlingen, Germany	Together with Helmut Metzner, of Tübingen, who had also worked with Melvin Calvin, Hartmut was its organizer
1980–1983	Research Program: "Enhancement of photosynthesis and the biological solar energy conversion"	International OECD (Organization for Economic Cooperation and Development) Research Program	Hartmut Lichtenthaler was one of its coordinators
1984–1987	Remote sensing of forest decline in USA and Germany	National Aeronautics and Space Administration, USA, and the German Aerospace Organisation, Oberpfaffenhofen	Hartmut had initiated it in 1984 and actively participated in it till 1987
1986	5th Congress of FESPP (Federation of European Societies of Plant Physiology)	31 August–4 September 1986, Hamburg, Germany	Hartmut was then President of FESPP (*see* Fig. 9)
1988	International Symposium on "Applications of Chlorophyll Fluorescence"	Held in June,1988, in Bad Honnef, Germany	Hartmut was its organizer
2005	International Symposium on Chloroplast Engineering	Held at the Rebeiz Foundation in Champaign, Illinois, in May, 2005	Hartmut was co-organizer with Tino Rebeiz Hartmut led the session on "Chloroplast isoprenoid lipids and the new plastidic DOXP/MEP isoprenoid biosynthesis pathway"
1990 and later	Research Programs of the EUREKA Research Initiative of the European Union	Examples are: "Laser-induced Fluorescence of Plants" as well as: "Quality Assessment of Agrofood by Fluorescence Imaging"	Hartmut has been an initiator of and participant of the two examples indicated and various others