



# David (Dave) Charles Fork (1929–2020): a gentle human being, a great experimenter, and a passionate researcher

Govindjee Govindjee<sup>1</sup> · Laurie Fork Peterson<sup>2</sup> · Kazuhiko Satoh<sup>3</sup> · Stephen Herbert<sup>4</sup> · Yaroslav de Kouchkovsky<sup>5</sup> · Ulrich Schreiber<sup>6</sup> · Norio Murata<sup>7</sup> · Gunnar Öquist<sup>8</sup> · Anthony W. D. Larkum<sup>9</sup> · Tetsuo Hiyama<sup>10</sup> · Joseph A. Berry<sup>11</sup>

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## Abstract

We provide here an overview of the remarkable life and outstanding research of David (Dave) Charles Fork (March 4, 1929–December 13, 2021) in oxygenic photosynthesis. In the words of the late Jack Edgar Myers, he was a top ‘*photosynthetiker*’. His research dealt with novel findings on light absorption, excitation energy distribution, and redistribution among the two photosystems, electron transfer, and their relation to dynamic membrane change as affected by environmental changes, especially temperature. David was an attentive listener and a creative designer of experiments and instruments, and he was also great fun to work with. He is remembered here by his family, coworkers, and friends from around the world including Australia, France, Germany, Japan, Sweden, Israel, and USA.

**Keywords** *Binghamia forkii* · Stacy French · E. Yale Dawson · Chromatic adaptation · Two light effect on photosynthesis · Dynamic membrane changes · 8th International Photosynthesis Conference · Carnegie Institution for Science · Spectrophotometry, oxygenic photosynthesis

✉ Govindjee Govindjee  
gov@illinois.edu

✉ Joseph A. Berry  
jberry@carnegiescience.edu

Laurie Fork Peterson  
lauriefork@yahoo.com

Kazuhiko Satoh  
satoh-k3@jcom.home.ne.jp

Stephen Herbert  
stephen.herbert@georgetown.edu

Yaroslav de Kouchkovsky  
yakouch@gmail.com

Ulrich Schreiber  
ulrichschreiber@gmx.de

Norio Murata  
murata@nibb.ac.jp

Gunnar Öquist  
gunnar.ouquist@umu.se

Anthony W. D. Larkum  
a.larkum@sydney.edu.au

Tetsuo Hiyama  
thiyama@athena.ocn.ne.jp

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

<sup>2</sup> Berkeley, CA, USA

<sup>3</sup> Department of Life Science, University of Hyogo, 3-2-1 Kohto, Kamigohri, Akogun, Hyogo 678-1297, Japan

<sup>4</sup> Georgetown University, Washington, DC 20007, USA

<sup>5</sup> Centre National de la Recherche Scientifique (CNRS), 7 Rue A. Pécard, 91190 Gif-sur-Yvette, France

<sup>6</sup> Julius-von-Sachs Institut für Biowissenschaften, Würzburg University, Julius-von-Sachs Platz 2, 97082 Würzburg, Germany

<sup>7</sup> National Institute for Basic Biology, Okazaki 444-8585, Japan

<sup>8</sup> Department of Plant Physiology, Umeå Plant Science Centre, Umeå University, 90 187 Umeå, Sweden

<sup>9</sup> Department of Plant Sciences, University of Sydney, Sydney, NSW 2050, Australia

<sup>10</sup> Department of Biochemistry and Molecular Biology, Saitama University, Saitama 338-8570, Japan

<sup>11</sup> Carnegie Institution for Science, 260 Panama Street, Stanford, CA 94305, USA

## Introduction

David C. Fork was both a great scientist and a wonderfully sweet human being. He followed in the footsteps of Louis N. M. Duysens, a great Dutch scientist (see Govindjee and Pulles 2016), who made the critical insight that there were two photoacts in photosynthesis using spectroscopy to show that lights of different colors could alternatively reduce and oxidize a cytochrome. This led him to posit that one photoact (PS II) pushed electrons and another (PSI) pulled them along an electron transport chain linking oxygen production to CO<sub>2</sub> fixation (for a history of the evolution of this scheme, see Govindjee et al. 2017). We provide, below, a summary (an overview) of David's research (see later for references). He greatly improved the spectroscopic tools that Duysens had used and went on to characterize other components of the chain such as plastocyanin and several b-type cytochromes, and worked on other absorbance changes (the electrochromic shift) that turned out to be related to the chemo-osmotic gradients that drive ATP formation. Dave also conducted important studies on the kinetics of electron transport reactions showing how temperature-dependent changes in the fluidity and phase of lipids affected the rate of diffusion of electron carriers in the chloroplast membrane. In work with thermophilic algae, he was able to show that membrane lipids played a role in determining the heat tolerance of photosynthesis. David's background as a naturalist led him to study the diversity of photosynthetic pigments in organisms other than spinach and *Chlorella*. He was fascinated by the range of pigments used by algae and cyanobacteria and how the organisms controlled the configuration of their pigment systems (chromatic adaptation) to achieve balanced excitation of the two photosystems in the specific light environments they inhabited. He also was able to demonstrate dynamic adjustments (state changes) that could rebalance the distribution of excitation between the two photosystems when the organism is confronted with short-term changes in light quality. All of this work involved a steady stream of collaborators who came to work with David (see the section on "Reminiscences"). He was a great listener and a creative designer of experiments. His laboratory was known as a place to take your ideas. If they were good, Dave would figure out a way to test them. In this remembrance, several of these collaborators have described their times in Dave's laboratory. In addition, his family and colleagues have documented his history and the personal qualities that so endeared him to them.

## Early life

David (Dave) Charles Fork was born on March 4, 1929, in Detroit, Michigan to Emma and Charles Fork. When Dave was young, the family moved to Brentwood, a suburb of

Los Angeles, California. In early 1940s, the Fork family moved to San Diego, where an internship at the San Diego Natural History Museum led to David's fascination with Plant Biology. Through the various plant collection trips in Baja California and Mexico that he took with his mentor, a renowned botanist and phycologist E. Yale Dawson (1918–1966), Dave developed an interest in studying plants and algae (For Dawson, see [https://en.wikipedia.org/wiki/E.\\_Yale\\_Dawson](https://en.wikipedia.org/wiki/E._Yale_Dawson).) Interestingly, during one of these trips, Dave discovered a new alga that was later named *Binghamia forkii* by Dawson, and described in 1952, by Paul C. Silva <https://www.marinespecies.org/aphia.php?p=taxdetails&id=372783> <https://www.marinespecies.org/aphia.php?p=taxdetails&id=372783>. Figure 1 shows a 2001 portrait of David Fork.

## Academic studies

In 1947, David C. Fork graduated from San Diego High School. After studying Liberal Arts and Sciences, particularly Biology, first at the University of California, Los



**Fig. 1** A 2001 photograph of David C. Fork; source: Laurie Fork Peterson; also see: <https://paltoononline.com/obituaries/memorials/david-c-fork?o=6830>

Angeles (UCLA) and then at the University of California, Berkeley, he received his B.S. in Botany in 1951. His academic studies were put on hold for a while because of the Korean War (1950–1953) when he served as an Officer of the Navy before beginning his PhD in Botany at UC Berkeley.

On the personal side, it was in California that Dave met Joan Mills (Jody) and they were married in 1958 (see Fig. 2).

David received his PhD in 1961, for work he had done under the mentorship of Francis T. Haxo (1921–2010; for Haxo, see <https://www.legacy.com/us/obituaries/pomeradonews/name/francis-haxo-obituary?id=21548665>, and Govindjee and Thorhaug 2022). David's very first research paper (Haxo and Fork 1959) dealt not only with the demonstration in cryptomonads, of high photosynthetic activity of 'phycoerythrins', but also of chlorophyll *c* and chlorophyll *a*, the latter result in contrast to those in red algae. After his PhD, David took up a postdoctoral fellowship (1960 to 1961) at the Carnegie Institution Department of Plant Biology at Stanford, where he was appointed a staff member in 1961. During this time, he also did research at Scripps Institution of Oceanography. Fork (1963) summarized both this newer research, as well as his PhD work, dealing with the function of accessory pigments in photosynthesis—not only of cryptomonads and red algae, but of brown algae, at

a conference held at Airlie House, Warrenton, Virginia; for a parallel presentation by one of the authors, see Govindjee (1963). This is where Govindjee and Fork met and discussed their results on the *Emerson Enhancement Effect and the Two Light Reaction Concept of Photosynthesis* in various algae—generating discussions that led to a long-term, close friendship.

Soon after his appointment at the Carnegie Institution of Washington (now Carnegie Institution for Science) at Stanford, led by world-renowned research scientist Charles Stacy French (1907–1995; see Govindjee and Fork 2006), Fork went overseas to study at leading photosynthesis laboratories in France, Germany, and the Netherlands. Upon his return, David set up a laboratory in a dark corner of Carnegie's basement. It was essentially a walk-in spectrophotometer with mirrors, lights, shutters, monochromators, and fast recorders like those you would see in a cardiologist's office. He implemented the most advanced technologies that he had learned from his European trip. The instruments were superbly suited for measurement of small changes in the absorbance or fluorescence of leaves, algae (or sub-cellular preparations from these) that occur during photosynthesis. In the Carnegie tradition, David built this setup himself with the help of the lab's engineering staff. Not only was this one of the best facilities for kinetic spectroscopy in the world at the time, David's combination of great insight and patience also attracted researchers from around the world to come to work with him. His lab became a place where new ideas came to be tested. A long string of new discoveries and new technical approaches followed. For the next four decades, Dave conducted research in photosynthesis until his retirement in 1995, as summarized below, and as described by his collaborators under *Reminiscences*.

### Research at the Carnegie Institution for Science (formerly Carnegie Institution of Washington), at Stanford, California

Dave's passion and research focused on the mechanism of oxygenic photosynthesis in plants and algae. Dave attracted many international scientists to do research with him over the years. We have divided his work chronologically to cover his research from the 1960s through the 1990s, and with a smaller number in the 2000s (after his retirement).

#### The 1960s

During this period, David had two major collaborators: the late Jan Ames (from The Netherlands; 1934–2001; see Hoff and Aartsma 2002) and Yaroslav de Kouchkovsky (from France). With de Kouchkovsky (see below for his *Reminiscences*), Dave provided one of the earliest and most



**Fig. 2** David and Jody Fork on their wedding day in 1958. Source: The Fork family



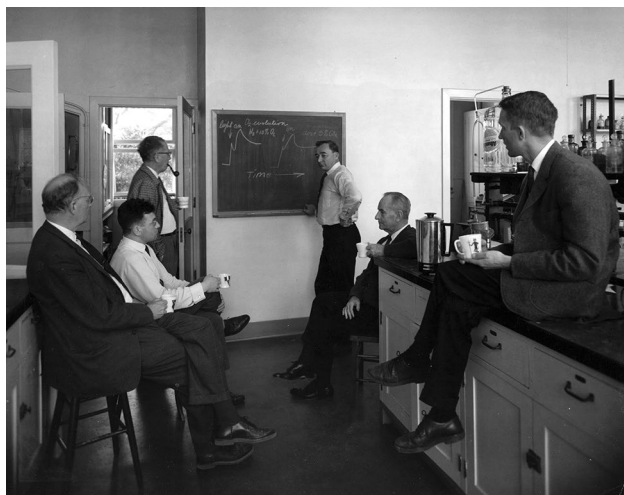
thorough clues about the possible role of plastocyanin (PC) which carries electrons from the Cytochrome *b<sub>6</sub>f* complex to Photosystem I; all this was detected and characterized by light-induced absorbance changes in PC (de Kouchkovsky and Fork 1964; cf. Fork and de Kouchkovsky 1968). In addition, Fork and de Kouchkovsky (1966) exploited information on the 515 nm absorbance changes—as related to the functioning of the Z-scheme (for related work on 520 nm (and 480 nm) absorption changes, and their relation to two light reaction scheme of photosynthesis in *Chlorella* cells, see Govindjee and Govindjee 1965).

Figure 3 shows David Fork in a group seminar in the laboratory where the late Stacy French and Yaroslav de Kouchkovsky were present, and Fig. 4 is a photograph of Dave with Jan Amesz, mentioned above, and Govindjee, one of the authors of this tribute.

Dave provided detailed kinetic information on (a) the function of cytochrome *f* and plastocyanin in the Z-scheme of red algae (Amesz and Fork 1967; for historical aspects of the Z-scheme, see Govindjee et al. 2017), and (b) the light-induced shifts, related to the proton motive force, in both the red and brown algae (Fork and Amesz 1967).

## The 1970s

During this period, David had a major collaborator: Norio Murata (from Japan; see his *Reminiscences*). We provide here just a glimpse of the research topics covered. With Norio Murata, David extended investigations on the kinetics of P700 (the reaction center of Photosystem I) and cytochrome *f* using samples enriched in Photosystem I



**Fig. 3** David Fork (sitting on a lab counter on the far right), in a group seminar at Carnegie, early 1960s. Left to right: C. Stacy French, Yaroslav de Kouchkovsky, Harold Milner, William Vidaver (at the blackboard), James H. C. Smith, and David Fork. Source: Carnegie Archives



**Fig. 4** Left to right: Govindjee, Jan Amesz (b.1934-d. 2001), and David C. Fork, 1980s, at a conference. Source: Rajni Govindjee's archives

(Fork and Murata 1971; Murata and Fork 1971). A major new idea was to exploit changes in temperature and to relate the observed changes (in photosynthesis and chlorophyll *a* fluorescence) to the physical state of the chloroplast membrane allowing one to understand the structure/function relationships, and to get a dynamic picture of photosynthesis functions in nature. To obtain a detailed picture of the contribution of Dave Fork, in this area, see *Reminiscences* by Murata, as well as their published papers: Fork and Murata (1977), Fork et al. (1979), Murata and Fork (1977a, b), and Murata et al. (1975).

In addition, during the 1970s, a collaboration began with Joseph (Joe) Berry also at the Carnegie Institute (see Pearcy et al. 1977); here, they studied the effects of growing *Atriplex lentiformis* at different temperatures on the thermal stability of its photosynthetic apparatus.

Figure 5 shows a 1977 group photograph of the scientists in the Department of Plant Biology at Carnegie Institution; this photo includes two of the authors of this paper: Norio Murata and Ulrich Schreiber. Dave (in checkered shirt) is in the bottom row. For an enlarged photo of Dave (from this group), see the Supplementary Material.

## The 1980s

This was the most productive period in Dave's research life. We shall be brief here, beginning with a glimpse of his work with Kazuhiko Satoh (see his *Reminiscences*), followed by those with Prasanna Mohanty (1934–2013; Tiwari et al. 2014; Naithani and Govindjee 2018); Gunnar Öquist (see his *Reminiscences*); Shmuel Malkin (1934–2017); Herbert et al. 2018; also see the “Reminiscence” of Herbert, and “the 1990s” section.





**Fig. 5** A 1977 group photograph of scientists working in the Department of Plant Biology at the Carnegie Institution of Washington. David Fork (in checkered shirt) is in the bottom row. Some others are: 1st row, (bottom row): Aaron Kaplan (4th from the left, leaning on the wall); 2nd row: Winslow Briggs (2nd from the left); Olle Bjotkman (3rd from the left); Malcolm Nobs (5th from the left, with his back against the wall); 3rd row: Stacy French (1st from the left);

George Bowes [4th (i.e., at the end) from the left]; 4th row: Jeanette (Jan) Brown (3rd from the left, close to the wall); Norio Murata (4th from the left); John Boynton (6th from the left); Murray Badger (9th from the left); 5th row, the top row: James (Jim) Ehleringer (2nd from the left); Alan Stemler (3rd from the left); Ulrich (Uli) Schreiber (5th from the left). Source: Ulrich Schreiber

### With Kazuhiko Satoh (Japan)

Together with Satoh (see his *Reminiscences*), Dave made great inroads in the area of regulation of excitation energy between the two photosystems including what is known as the “State I to State II” changes, or the reverse, i.e., “State II to State I” (Fork and Satoh 1983; Satoh and Fork 1983e, f); further, Satoh and Fork (1983g) related these changes to cyclic electron flow. Then, the two went deeper and presented newer mechanisms for adaptation of red algae to changes in the intensity and the wavelength of light (see Satoh and Fork 1983b, c, d). Finally, Fork and Satoh (1986) published a comprehensive and balanced review of this field of how plants and algae regulate energy distribution and of redistribution between the two pigment systems. In addition, Satoh and Fork provided detailed information on questions such as the following: (i) how does excess light



**Fig. 6** David Fork at his spectrophotometer in 1983. Source: Kazuhiko Satoh

under anaerobic condition affect intact chloroplasts (Satoh and Fork 1982); (ii) how can one gauge the redox state of plastoquinone through chlorophyll *a* fluorescence transient (Satoh and Fork 1983a); (iii) what does excess salt do to the primary reactions of photosynthesis (Satoh et al. 1983); (iv) what does osmotic tissue dehydration do to the excitation energy transfer in red algae (Smith et al. 1986); (v) how does red light stimulate bioluminescence in dinoflagellates (Sweeney et al. 1983); and lastly (vi) how does delayed light emission change with time in thermophilic cyanobacteria (Satoh and Fork 1983b). Although definitive answers to most of these questions are still elusive, they indicate the breadth and depth of the research that Satoh and Fork brought before us in a very short time! Fig. 6 shows Dave's photograph with the instrument he had built and used when Kazuhiko Satoh was there.

#### With the Late Prasanna Mohanty (India)

Together with Mohanty (and Jerry Brand & Satoshi Hoshina), David followed his passion of understanding how temperature changes, especially at high temperatures, affect the absorption, fluorescence (both prompt and delayed), and excitation energy transfer steps, particularly in the cyanobacterium *Anacystis nidulans* (see e.g. Hoshina et al. 1984; Fork et al. 1985; Mohanty et al. 1985a, b). In addition, new information was provided by Brand et al. (1983) and by Mohanty et al. (1985a, b) on the inhibitory effects of the removal of calcium ions on the photochemical events in Photosystem II, thus emphasizing its key role in the so-called 'state changes' i.e., regulation of energy transfer between Photosystem I and II. Lastly, Fork and Mohanty (1986) provided an overview of not only such events in cyanobacteria, but in red algae and cryptomonads including what was known from the earlier work of David with Kazuhiko Satoh.

#### With Gunnar Öquist (Sweden)

The idea of how water deficit (by desiccating the samples) affects excitation energy transfer between the two Photosystems was pursued in the red alga *Porphyra perforata* (Fork and Öquist 1981; Öquist and Fork 1982a) as well as in other organisms (Öquist and Fork 1982b)—all in the overall area of how the environment controls individual steps of photosynthesis and what we can learn to improve overall photosynthesis and productivity. Towards this goal, Öquist et al. (1981) worked even at the level of chlorophyll protein complex from the cyanobacterium *Synechococcus lividus*, and Fork et al. (1982) looked at the Photosystem I emission properties at room temperature of the red alga *Porphyra perforata*. (See *Reminiscences* by Gunnar Öquist.)

#### With the late Shmuel Malkin (Israel), and a few others (including Govindjee, one of the authors)

The focus on exploiting the effects of temperature and water on photosynthesis was continued by these coworkers. However, the effect of excess light and differences between sun and shade plants was another focus. Fork and Govindjee (1980), Malkin and Fork (1981) and Malkin et al. (1981) provided important information on significant differences between the size of the 'photosynthetic units' in sun and shade plants, this being twice as large in 'shade' than in 'sun' plants! At the same time, Govindjee et al. (1981) provided a simple tool for looking at water potential of leaves—adapting the well-known Kautsky effect, i.e., chlorophyll *a* fluorescence transient (see e.g., Govindjee 1995, for an overall historical review). The key external factor, temperature, dominated David's research: (i) Fork et al. (1981) determined phase transition temperatures in thylakoids; (ii) Harvey et al. (1982) related membrane lipid phase-separation information with frost tolerance in cereals, which provided important practical information; (iii) using heat-stressed chloroplasts, Williams et al. (1986) and Fork et al. (1987) showed that there was a selective photobleaching of Photosystem I related chlorophylls when, in general, it is Photosystem II that is known to be affected; (iv) with Stephen Herbert (one of the authors), Fork et al. (1986) showed that protection against excess light, both in plants and algae, is through increased radiationless (i.e., by internal conversion) losses [see Chapters in Demmig-Adams et al. (eds) 2014]. These observations were followed by (a) Yamagishi and Fork (1987) who provided detailed information on electron transport steps on the acceptor side of Photosystem II in thermophilic cyanobacterium *Synechococcus* (for earlier information, see Govindjee et al. 1985); and (b) Bose et al. (1988) provided important physiological information on how the recovery of sun and shade species of red alga *Porphyra* takes place, as measured through fluorescence.

#### The 1990s and beyond

During this period, collaboration with Norio Murata (see "The 1970s") and with Shmuel Malkin (see the discussion for the 1980s period) continued, but it was *so-to-say* the era of Stephen Herbert (also see his *Reminiscences*) and a few others, e.g., Arthur (Art) Grossman, Joseph (Joe) Berry and Guy Samson. Fork's focus on temperature and physiology continued during this period. Using light emission measurements, Fork and Murata (1990) provided new data on the effect of light intensity on the low temperature limit of photosynthesis; Terzaghi et al. (1990) provided a detailed survey of low and high temperature limits of Photosystem II of a large number of photosynthetic organisms.



Further, during the 1990s, a novel technique—namely photoacoustic spectroscopy (measurement of sound waves generated when light is absorbed by chlorophyll) was exploited to measure energy storage in algae and higher plants (Herbert et al. 1990). Fork and Herbert (1991) even made a new cell for these measurements, and Fork and Herbert (1993a) provided a comprehensive review of what had been learned using this fascinating new technique. The overall thrust, however, was on further detailed understanding of (a) the electron transport and the carriers—particularly of the cytochromes; and (b) the energy distribution and redistribution between the two photosystems.

For electron transport, Laudénbach et al. (1990) established that cytochrome  $c_{553}$  is not required in the cyanobacterium *Synechococcus*; Samson and Fork (1991, 1992) provided detailed information on the intricate role of cytochrome  $b_{559}$  in photosynthesis; and Fork and Herbert (1993b) provided a thorough overview of both electron transport and phosphorylation by Photosystem I in plants as well as cyanobacteria. For a detailed picture of cyclic reactions in PSI, see Herbert et al. (1995). On the other hand, to understand the mechanism of energy distribution and redistribution among the two photosystems in the red alga *Porphyra perforata*, Malkin et al. (1990) used photoacoustics; and Fork et al. (1991) did the same for the brown alga *Macrocystis pyrifera*. An earlier picture of the above process was, however, reviewed in an authoritative review by Fork and Satoh (1986).

Dave's interest in the physiology of photosynthetic systems is revealed by his quest to answer the following questions: (i) how does lack of super oxide dismutase (SOD) damage the photosystems? (see Herbert et al. 1992; Samson et al. 1994); (ii) what changes does macronutrient deprivation produce in the photosynthetic apparatus of cyanobacteria? (see Collier et al. 1994); and (iii) what biochemical changes take place during frost tolerance of plants? (see Harvey et al. 2006, with Joe Berry). Lastly, with the renowned photobiologist, Harry Smith, Dave experimented with the possible role of 'phytochromes' in photosynthetic acclimation to light (Smith and Fork 1992; Smith et al. 2006) and in light-driven (phototactic) movement of bean leaves (Koller et al. 1996).

Dave had great regard for the late C. Stacy French, who had hired him and supported and encouraged Dave's independent research. See Fork (1996) and Govindjee and Fork (2006) for Tributes to Stacy French. In addition, Dave appreciated William A. Arnold's early measurements on the minimum quantum requirement of oxygen evolution by calorimetry (Malkin and Fork 1996; for details on the controversy of the quantum requirement, see Nickelsen and Govindjee 2011).

We end this section by mentioning that Dave had taken a sabbatical to collaborate with Norio Murata at the National

Institute for Basic Biology in Japan and with Anthony (Tony) Larkum at the University of Sydney in Australia. As a member of an international community of plant physiologists, he enjoyed many decades-long collaborations and friendships with colleagues from around the world, and he did this even from the early days of his research. He was always open to discussing new ideas and was particularly known for suggesting how to test these ideas and for his generosity in opening his lab and donating his time to do the experiments—if, of course, he thought it a "good idea." One of us (Joe Berry) remembers his excitement when sitting at Dave's elbow in the dark lab while the answers to his questions spooled off the transient recorder on to the floor. That was real science!

## Reminiscences

### 1. Laurie Fork Peterson (lauriefork@yahoo.com)

My sisters, Patty, Susie, and I remember our father, Dave, with deepest affection. He gave us the ultimate gift—a lifetime of his love and affection; he was always there for us—and because of this, he lives forever in our hearts.

Dave was a devoted father, a loving husband to our mother, Jody, for 56 years, a fun-loving brother, and a sweet grandfather. Friends describe him as "the salt of the earth" and "a true gentleman." With a playful sense of humor and indefatigable energy, he built his life around the things he loved most—his family, the outdoors, and beauty in art, music, and nature. One friend remarked, "I learned a tremendous amount from Dave—about empathy, kindness, and how to live a rich and wonderful life. He inspired me and gave me a sense of how to build a family on a foundation



**Fig. 7** A 1980s photograph of David Fork with his family on the Forsyth Peak. Left to right: Jody, Dave, Patty, Laurie, and Susie. Source: Archives of the Fork family



**Fig. 8** David Fork with his family in Woodside, California in 2005. Left to right: David, Patty, Laurie, Jody, and Susie, and three grandkids in tow. Source: Archives of the Fork Family

of gentleness and compassion.” Dave’s sister, Kathy Coull, remarked, “He meant the world to me. He had a brilliant mind and a great sense of humor.”

Over the years, our parents shared their mutual love of the outdoors, taking us on many adventures—camping and backpacking in the Sierra Nevada; canyoneering in Utah, and traveling in Europe, Australia, Asia, and the Pacific. Always the inveterate botanist, Dave imparted his knowledge of flora and natural history to us wherever we went.

Figure 7 shows David and Jody with their three daughters: Patty, Susie, and Laurie (author of this Reminiscence) on a backpacking trip in Yosemite National Park at the top of Forsyth Peak in the 1980s.

Dave was a passionate mountaineer, hiker, and above all, a backpacker. He took his first “knapsack” trip in the Sierra Nevada in the late 1940s and after that was hooked for life. He returned to the mountains every summer with friends and family for rejuvenation and inspiration until he was 83. Figure 8 shows him at an outing (picnic) in Woodside, California, 2005.

During the 1950s, Dave climbed many of the well-known spots in the Yosemite Valley, as well as the country’s highest peaks located in the southern Sierra. Over the course of his life, Dave had the pleasure of climbing Australia’s Uluru (Ayer’s Rock) once, California’s Mount Whitney twice, and Japan’s Mt. Fuji three times—and always reminded us about the Japanese proverb, *A wise man climbs Fuji once. Only a fool climbs it twice.*

A few months before he passed away, Dave and I were driving through Stanford campus, and although he wasn’t feeling well at the time, he suggested that we pull into the parking lot at Carnegie. We sat in the car for a long while as Dave reminisced about the nearly four decades spent there—he talked fondly about the many people with whom he had



**Fig. 9** Yaroslav de Kouchkovsky (right) with David Fork (left), Stockholm, 1989. Source: Archives of de Kouchkovsky

worked, how the wonderful friendships with Carnegie staff and scientists from all over the world had enriched his life, and how grateful he was for a lifetime in science.

## 2. Yaroslav de Kouchkovsky (yakouch@gmail.com)

My first meeting with David Fork took place in Gif-sur-Yvette (France), in July 1962, on the occasion of the International Photosynthesis Conference, organized by the CNRS (*Centre National de la Recherche Scientifique*). The laboratory (*Laboratoire de Photosynthèse*) where I was working was located on this CNRS campus, near Paris, and we had organized a visit of the conference participants to our laboratory so, Dave came; he and I had been working, independently, on topics related to oxygen release during photosynthesis. I had adapted a sensitive and (relatively) fast Clark electrode, and Dave was using an electrode developed by Francis Haxo (1921–2010; see Govindjee and Thorhaug 2022). Dave and Stacy French (1907–1995; see Govindjee and Fork 2006) were genuinely interested in all these developments, and, soon thereafter, Stacy French invited me to spend a year at the Carnegie Institute at Stanford. It was a great opportunity, as this center had an excellent reputation and offered us great possibilities for discussing our results with the research group there! When I arrived at Stanford, after a somewhat independent start, Dave and I decided to cooperate directly. I wanted to demonstrate that a chloroplast protein, plastocyanin, discovered shortly before by Sakae Katoh, was functionally located between the two photosystems, which we indeed established (de Kouchkovsky and Fork 1964; Fork and de Kouchkovsky 1968). We then firmly settled the relationship between the oxygen release and the



photoinduced electrochromic effect on photosynthetic pigments, around 515–520 nm, which was considered to be specific to Photosystem II (PSII). However, our results suggested that a portion, albeit minor, of the measured signal was attributable to PS I (Fork and de Kouchkovsky 1966). Of course, all these results had to be put in the context of the time. Our results and discussion, in our papers, show the excellent cooperation that existed between us. While performing the experiments, we often had fun and joked a lot; I taught Dave some French expressions, and he taught me the American way of saying the same. On the other hand, we were both great lovers of nature— he and his family were attracted mainly to the mountains and I was drawn to encountering and learning about various human cultures. This is how our relationship became a real friendship. Dave and his wife Jody (alas also deceased) hosted and supported me at the beginning of my arrival. We also had some family exchanges, especially when their eldest daughter, Laurie, came to spend a year in France or when I visited them in California, once with my wife (Françoise 1939–2021). That is why I was deeply affected, first by Jody's loss, then by Dave's illness and death. When my wife passed away in 2021, Laurie, whom we had seen with all her family 2 years earlier in Paris, showed me how deep the affinity was between Dave's family and mine.

I end my *reminiscence* with a photo of Dave and me taken during a 1989 conference in Stockholm (Fig. 9); also see Supplementary Material.

### 3. Ulrich Schreiber (ulrichschreiber@gmx.de)

It was during 1976–1978 that I was at the Department of Plant Biology in the Carnegie Institute of Washington (Stanford, CA), where I enjoyed friendship with David Fork, and others including Norio Murata (from Japan), Mordhay Avron (from Israel; 1931–1991; see Gromet-Elhanan 1992), Aaron Kaplan (from Israel), Murray Badger (from Australia), Alan J. Stemler (Govindjee's former PhD student), Jeanette Snyder Brown (1925–2014; see Briggs and Govindjee 2016), Winslow Briggs (1928–2019; <https://news.stanford.edu/2019/02/15/plant-biologist-winslow-briggs-dies-90/>), Charles Stacy French (1907–1995; see Govindjee and Fork 2006), Joseph (Joe) Berry, and Olof (Olle) Eric Björkman (1933–2021). Dave was most knowledgeable about biophysical aspects of photosynthesis, and we shared a particular interest in optical measurements. I remember the stimulating discussions we had at lunchtime, sitting outside in the garden on a bench. When I arrived at the Carnegie, coming from the Lab of William (Bill) Elliott Vidaver 1921–2017 (see Burr et al. 2018), I brought with me a basic custom-made multi-branched fiberoptics system for measuring chlorophyll *a* fluorescence, and Dave was very helpful in providing me with all the accessories that

were required for studying ATP-induced reverse electron transport (done with Mordhay Avron) and the heat-induced increase of fluorescence yield (done with Joe Berry). While he himself was too busy to participate, he was always very interested in the results, which was rewarding for me. I have very fond memories of Dave Fork; we miss him, as well as Mordhay Avron, Olle Björkman, Jeanette Brown, and Stacy French.

### 4. Kazuhiko Satoh (satoh-k3@jcom.home.ne.jp)

I worked with David C. Fork for 2 years, from 1980 to 1982. Before that time, while I was in Japan, he was already teaching me English. For me, he seemed to write very good papers, and so, I would translate his papers first into Japanese and then back to English, and finally I would compare the back-translated papers with Dave's original ones! This was one way I learned how to write in English. While I was in Dave's Lab at the Carnegie Institution of Washington (CIW) at Stanford, now Carnegie Institution for Science, we regularly discussed our joint research. I vividly remember that he was patient enough to hear my bad (poor) English. Fortunately, I was able to do many experiments, using his excellent '*hand-made*' instruments, and then, I could draft many research papers, which he edited before they were submitted for publication (see below). Now, a bit about Dave's instruments: I was pleasantly surprised to have, from him, various useful kinds of equipment he had constructed for measurements of, e.g., light-induced redox changes of cytochrome *f*, millisecond (ms) delayed chlorophyll *a* fluorescence; in addition, Dave had a keen interest in various physiological phenomena related to oxygenic photosynthesis—involving effects of salinity (see Satoh et al. 1983), and of dehydration (Smith et al. 1986) on plant performance. Further, Dave's work included effects of different colors of light on bioluminescence, the latter done with the late Beatrice Sweeney (1914–1989; see Sweeney et al. 1983).

We began our collaborative research using isolated intact chloroplasts, and for this, we chose the alga *Bryopsis corticulans* (<https://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi?id=325651>) since it was easy to get intact chloroplasts from this organism. For this and other research, Dave contacted scientists at Hopkins Marine Station <https://hopkinsmarinestation.stanford.edu/> to help us. For our results on photoinhibition of the two photosystems, and on the redox state of plastoquinone in *Bryopsis*, see Satoh and Fork (1982), and Satoh and Fork (1983a), respectively. Later, this contact led to new research on desiccation tolerance of marine algae and much more. I personally know that it was not just me, but many other scientists, who have enjoyed collaborating with Dave. Furthermore, Dave was also one of the few scientists who recognized the usefulness



**Fig. 10** Left to right: David Fork and Kazuhiko Satoh, at the 8th International Conference on Photosynthesis Stockholm, Sweden, 1989; for presentations at this conference, see Baltscheffsky (1990). Source: Kazuhiko Satoh

of working with thermophilic cyanobacteria, which became a very important model for future photosynthesis research.

Dave and I studied, quite thoroughly, State I–State II transition (i.e., regulation of light energy distribution between Photosystem I and Photosystem II) in thermophilic cyanobacteria (Fork and Satoh 1983), in the red alga *Porphyra* (Satoh and Fork 1983b, 1983c, 1983d), in the green alga *Scenedesmus* (Satoh and Fork 1983e), and in spinach, a higher plant (Satoh and Fork 1983f). For the relationship of state changes to cyclic reaction in PSI, see Satoh and Fork (1983g). To cap it all, Dave wrote a thorough review on the exciting topic of ‘state changes’—regulation of excitation energy distribution and redistribution between Photosystem I and II (Fork and Satoh 1986).

I am writing this *remembrance* because I want to give heartfelt thanks to David C. Fork for his kindness and friendship, for giving me the opportunity to have a wonderful life in science, and for collaboration with him in the Department of Plant Biology, at the Carnegie Institution of Sciences, at Stanford, California. I end my reminiscence by showing a 1989 photograph of Dave with me (see Fig. 10).

##### 5. Norio Murata (murata@nibb.ac.jp)

I joined the Carnegie Institution of Washington, Department of Plant Biology (hereafter, abbreviated as Carnegie), in 1969, and stayed there as a Carnegie Fellow for one and a half years. At that time, members of the department were C. Stacy French (Director), Jannette (Jan) Brown, David (Dave) C. Fork, Olle Bjorkman, and a few others. Some years later,

I visited Carnegie four times for a period of 3 months each. During the stay there, I did research on (i) characterization of fraction 1 and fraction 2 particles derived from spinach chloroplasts after treatment by French press; and (ii) temperature-dependent characterization of photosynthesis in relation to the physical phase of thylakoid membrane lipids.

##### *Fraction 1 and fraction 2 particles*

The French Press, which was a powerful equipment for disintegrating cells and organelles into small fragments, was constructed by Stacy French in the department. Before my arrival, some members of the department had used the French Press to disintegrate thylakoid membranes to fragments of different sizes and separated them by centrifugation in a sucrose-density gradient, fragments of light and heavy particles, i.e., fraction 1 and fraction 2 particles, respectively. Jan Brown and I (see Murata and Brown 1970) characterized these particles by examining their photochemical activities. Our results revealed that fraction 1 particles were active in photochemical reaction 1 (Photosystem I), as determined by the NADP<sup>+</sup> reduction in the presence of diuron (DCMU) and an electron-donating system, whereas fraction 2 particles were active in both photochemical reactions 1 and 2, the latter determined by the oxygen evolution in the presence of ferricyanide (Murata and Brown 1970).

Dave Fork had developed an elegant electro-optical system for the measurement of light-induced absorbance changes, which was a method to investigate the oxidation/reduction reaction of components in the photosynthetic electron transport and, in addition, light-induced changes in chlorophyll *a* fluorescence. Using this equipment, Dave and I studied the oxidation/reduction reaction of P700 and cytochrome *f* in fraction 1 particles (Fork and Murata 1971). This study was extended, and Dave and I measured the reduction of cytochrome *b* as well as the light-induced spectral shift of carotenoids, at 515 nm (Murata and Fork 1971).

##### *Physical phase of thylakoid membrane lipids*

After the study of fraction 1 and 2 particles, Dave and I started a new topic of research, namely, *How does the physical phase of thylakoid membrane lipids affect temperature-dependent characteristics of photosynthesis and related reactions?* The most suitable to this study was the research condition of Carnegie and, in particular, the electro-optical equipment of Dave, with which changes in light absorption and chlorophyll *a* fluorescence could be measured at various temperatures. In addition, algal cells and plants could be cultivated at designated temperatures in a cultivation room at Carnegie. In this series of study, Dave and I selected several species of organisms with different temperature characteristics, such as the mesophilic cyanobacterium *Anacystis nidulans* (now *Synechococcus* species PCC 7942), the thermophilic cyanobacterium *Synechococcus lividus*, the thermophilic red alga *Cyanidium caldarium*, and chloroplasts from cold-tolerant plants such as spinach and lettuce.



### *Anacystis nidulans*

During 1974, Dave and I examined, under technical support from other research groups, the physical phase of lipids in thylakoid membranes that had been isolated from *Anacystis nidulans* cells by a spin labeling technique. The results of these measurements showed that the lipid phase transition between the liquid-crystalline (fluid) state and the phase-separation state (mixed solid–liquid-crystalline state) occurred at 13 °C and 24 °C in thylakoid membranes from cells that had been grown at 28 °C, or 38 °C, respectively. Then, Dave and I studied redox reactions of components involved in the photosynthetic electron transport at various temperatures in the intact cells of *Anacystis nidulans*. The result of this study showed that, at the temperature of lipid phase transition, a break point appeared in the Arrhenius plot of the rates of the photosynthetic oxygen evolution, the reduction of P700<sup>+</sup> (the oxidized form of Photosystem I reaction center), and the state transitions of pigments at about 12 °C and 22 °C in cells grown at 28 °C and 38 °C, respectively. These results suggested that the temperature of phase transition depends on the temperature of growth and that the lipid phase of thylakoid membranes strongly influences the photosynthetic rate and related reactions that occur in thylakoid membranes (Murata et al. 1975).

Dave and I further demonstrated that the temperature-dependent changes in the yield of chlorophyll *a* fluorescence had a peak at the phase transition temperature of thylakoid membrane lipids in *Anacystis nidulans*. In contrast, such a peak was not observed in the room temperature range in the fluorescence of allophycocyanin in cells that had been grown at different temperatures, and that of chlorophyll (Chl) *a* as well (note that we had extracted and resolved chlorophyll *a* in 80% acetone). These results suggested that the yield of chlorophyll *a* fluorescence was a suitable method for measurement of the phase transition of thylakoid membrane lipids (Murata and Fork 1975).

In parallel, Dave and I performed similar experiments with chloroplasts isolated from spinach, lettuce, and tomato plants that had been grown at different temperatures. In contrast to the results on *Anacystis nidulans* cells, these chloroplasts did not show such a maximum of chlorophyll *a* fluorescence and a break point in the Arrhenius plot in the room temperature range (Murata et al. 1975; Murata and Fork 1975).

### *Cyanidium caldarium*

In 1976, Dave and I worked on the temperature dependence of the light-induced spectral shift of carotenoids at 515 nm and the oxidation reduction reactions of cytochrome *f* in relation to the physical phase of thylakoid membrane lipids in the thermophilic red alga *Cyanidium caldarium*. Maxima in chlorophyll *a* fluorescence in this alga appeared at about 10 °C and about 8 °C in cells that had been grown at 45 °C and 38 °C, respectively. The Arrhenius plot of the

dark decay of the spectral shift of carotenoids and of the dark reduction of cytochrome *f* had break points, which corresponded to the temperatures of fluorescence maxima. These results suggested that the transition of the physical phase of membrane lipids between the liquid-crystalline and phase-separation states occur at these temperatures, and that the electron transport reactions and the relaxation steps of membrane potential (permeability to ions) were greatly affected by such a phase transition in this alga (Fork and Murata 1977). Then, Dave and I studied the kinetics of the light-induced spectral shift of carotenoids in *Cyanidium caldarium* at various temperatures. Below the temperature of phase transition, the dark recovery of the spectral shift after several seconds of actinic illumination had both fast- and slow-decay components. However, above the phase transition temperature only the slow-decay component was observed. These results of the spectral shift of carotenoids suggested that the thylakoid membrane becomes leaky to the ions when the lipids are in the phase-separation state (Murata and Fork 1977a).

### *Spinach and lettuce*

In 1976, Dave and I also studied the temperature dependence of chlorophyll *a* fluorescence in spinach and lettuce chloroplasts at sub-zero temperatures. The maximum of chlorophyll *a* fluorescence appeared at –31 °C in both spinach and lettuce chloroplasts. Since the occurrence of a maximum in the temperature versus fluorescence curve was an indication for the transition of the physical phase of thylakoid membrane lipids, as mentioned above, these findings suggested that the phase transition of thylakoid membrane lipids occurs at low temperatures (~ –30 °C) in chloroplasts of higher plants (Murata and Fork 1977b).

### *Synechococcus lividus*

During my last visit to Carnegie in 1977, Dave and I studied the effect of growth temperature on the temperature dependence of light-induced redox reactions of cytochrome *f* and of the state transitions in the thermophilic cyanobacterium *Synechococcus lividus*, which had been grown at 55 °C and 38 °C. The Arrhenius plot of the transient reduction of cytochrome *f* during illumination by actinic light that excited both pigment systems (I and II) revealed breaks near 43 °C and 26 °C for cells grown at 55 °C. In cells grown at 38 °C, these breaks occurred near 37 °C and 28 °C, respectively. The shift from the pigment State 1 to State 2 also showed characteristic breaks in the Arrhenius plot at 44 °C for cells grown at 55 °C and at 37 °C, and at 25 °C for cells grown at 38 °C. The break points in the Arrhenius plot of the pigment state transitions as well as of the cytochrome *f* reduction were related to the phase transition of thylakoid membrane lipids as studied by the temperature dependence of chlorophyll *a* fluorescence. Independently, in Japan, N. Sato and I studied variations in fatty acid composition with growth temperature in *Synechococcus lividus*. When the growth

temperature was lowered from 55 to 38 °C, the level of saturated (solid) fatty acids 18:0 and 16:0 decreased while the level of unsaturated (fluid) fatty acids 18:1 and 16:1 increased. These changes in saturation/unsaturation levels of fatty acids in thylakoid membrane lipids were compatible with the shift in phase transition temperature due to growth temperature (Fork et al. 1979).

#### Ten years later

In the mid-1980s, Dave and I, again, had a pleasant collaboration and renewal of our friendship. In 1985, I was appointed as a Professor at the National Institute for Basic Biology, Okazaki, Japan and directed a new laboratory. In 1987, I invited Dave to work together again in this new place. He visited us and stayed there with his family for 4 months. He and I studied a newer topic, *The effect of light intensity on the assay of the low temperature limit of photosynthesis using msec delayed light emission*. Steady state millisecond delayed fluorescence (DLE) of intact leaves and cyanobacterial cells was measured continuously with a Becquerel-type phosphoroscope, while cooling the system to near 0 °C or heating it from low to high temperatures. The temperature of maximum DLE depended upon the light intensity the samples were exposed to. In *Anacystis nidulans* cells that had been grown at 28 °C and 38 °C, the DLE maximum appeared near 15 °C and 23 °C, respectively, which were the temperatures where the phase transition between the liquid-crystalline and the phase-separation state occurred in thylakoid membrane lipids in these cyanobacterial cells (Fork and Murata 1990).

#### Importance of the collaborative research

This series of studies in collaboration between Dave and me indicated that the lipid phase of thylakoid membranes was critically important for photosynthetic organisms to perform photosynthesis. In addition, it was particularly important in stimulating the following research on the mechanism of cold sensitivity as well as the genetic manipulation of cold tolerance in plants and cyanobacteria (Wada et al. 1990; Murata et al. 1992).



**Fig. 11** Left to right: Norio Murata., David Fork, and Satoshi Hoshina at the 8th International Conference on Photosynthesis Stockholm, Sweden, 1989. Source: The Fork family

#### Deep gratitude from my heart

During the work in collaboration, Dave was, at all times, extremely kind, friendly, and helpful. The major reason for our successful collaboration was David's distinguished personality and his deep insight into experimental design. I always acknowledged his constant support. We all miss him dearly. Figure 11 shows my 1989 photograph with Dave Fork and Satoshi Hoshina.

#### 6. Gunnar Öquist (gunnar.ouquist@umu.se)

David Fork was a great scientist and a good and inspiring friend. I will always remember our stimulating scientific discussions, but also our trustful exchange of experiences and views on a more personal level. I am deeply grateful to Dave, who made my sabbatical year of 1980 most rewarding.

Upon my arrival at the "Carnegie" (Stanford), David Fork and I soon identified a common interest: to study the function of photosynthesis in desiccation tolerant organisms. Dave had already some experience working with the desiccation tolerant intertidal red alga *Porphyra perforata*, studying its Photosystem I function upon drying, and I had some experience in fluorescence analyses of the lichen *Cladonia impexa*, showing enhanced Photosystem I emission upon loss of water.

For most of my sabbatical year at the Carnegie, I was with Dave in front of his machine in the basement of the old Carnegie building analyzing the effects of desiccation on photosynthesis. Our favorite was *Porphyra perforata* that we had collected on Friday afternoons near Pigeon Point, north of Santa Cruz, California; thus, we had fresh algal thalli ready for experiments the following weeks. A typical day was to work with experiments until about 3 pm, when we went out in the sun with a cup of coffee to analyze recorded data and to make plans for the next day. This was the highlight of the day and we both looked forward to test our ideas the next day. Analyses of the 77 K fluorescence emission and excitation spectra of *Porphyra* showed that, upon desiccation, PSII was virtually "put into darkness", although the thallus, upon low tide, was exposed to full sunlight! We (Öquist and Fork 1982a) concluded that this was achieved by an increased excitation energy transfer of light absorbed by phycoerythrin to Photosystem I (PSI), mediated both by an increase of PSI absorption cross section and by an increased spill-over of excitation energy from PS II. Rewetting the thalli reversed observed changes within minutes. Our conclusion was that PSI upon drying acts as a sink for excess excitation energy, thus protecting PSII from photodynamic damages.

At about the same time, George Hoch, from the University of Rochester, visited Carnegie and joined us in our work with *Porphyra*, showing that, even at room temperature, this alga had a pronounced long wavelength PS I fluorescence band at 730 nm (Fork et al. 1982). Based on this observation,



we were then able to qualitatively confirm that *Porphyra* reacted at physiological temperatures to desiccation in the same way as observed earlier (Fork and Öquist 1981) at 77 K, i.e., an increased energy transfer to PSI.

To increase our understanding of how desiccation affects the distribution of excitation energy between the two photosystems in different desiccation tolerant species, we extended our studies to the liverwort, *Porella navicularis*, which unlike *Porphyra*, lives in a very shaded habitat; and to *Trebouxia pyriformis*, a green lichen alga, grown at low light intensity (Öquist and Fork 1982b). Like in *Porphyra*, there was a pronounced loss of PSII fluorescence emission upon desiccation of *Porella*, but without increased energy distribution to PSI. The response of *Trebouxia* to desiccation was intermediate between that of *Porphyra* and *Porella*. We ascribed the different responses of the species to their different habitats, i.e., exposed to sun versus grown in deep shade.

Dave had earlier studied the relation between the physical state of the thylakoid membrane lipids and photosynthetic functions. Together with Siegrid Schoch, from München University, and Gunilla Malmberg, from my laboratory in Sweden, who joined us for a couple of months at Carnegie, we analyzed how temperature affected the SDS solubilization of chlorophyll protein complexes from a thermophilic cyanobacterium, *Synechococcus lividus*, grown at 38 °C and at 55 °C (Öquist et al. 1981). We showed that the phase transition temperatures were critical for the solubilization of chlorophyll protein complexes, particularly so for the bulk complex derived from PS I, which required a solubilization temperature above the transition temperatures, while the complex representing PS II was less temperature-dependent. We considered the heat stability of the complexes as a way for *Synechococcus* to adapt to high temperatures, enabling it to grow.

7. Anthony (Tony) William Derek Larkum (a.larkum@sydney.edu.au)

I had admired David Fork's work on photosynthesis from the 1970's onwards. We became friends when David began to work on red algae around early 1980. Together with Roger Hiller and Ross Lilley, in Sydney (Australia), we began to explore the light reactions of intact red algal chloroplasts and the associated pigment proteins and linkage to phycobiliproteins. We were lucky in being able to work on the giant-celled red alga, *Griffithsia monilis*, from which we were able to extract whole rhodoplasts. This was an exciting time; and David Fork with Stephen (Steve) Herbert at the Carnegie Institution (at Stanford, California) began to look at photosynthetic reactions in another set of red algae using Dave's home-built oxygen electrode and fast spectral techniques. David also worked with many other top scientists including the late Jan Ames (1934–2001), from the

Netherlands, and Kazuhiko Satoh & Norio Murata (from Japan). From these studies we concluded that the phycobilisome, the large, water-soluble protein, composed of phycoerythrin, phycocyanin and allophycocyanin and linker proteins, is connected to both photosystem I and II, but is also easily disrupted.

During 1987/1988, David Fork (with his family) spent a 6-month sabbatical with me in Sydney. Fortunately, I had a fellowship from the Australian Coral Reef Society to work at the Lizard Island, so David and family accompanied me to the Great Barrier Reef area. We had a wonderful time together. At that time, *Ostreobium*, the skeletal-dwelling green alga of massive corals, was the center of interest for a number of marine biologists; we extracted this alga from the skeletal remains and worked on the first chlorophyll-proteins to be isolated from this organism (Fork and Larkum 1989). I particularly remember a magnificent trip that we all took to the outer Barrier about 30 km from the Lizard Island, diving on the outer side of this barrier on this flat calm day! (See Supplementary Material for a photograph from that time.) One could look down through wonderfully transparent water to a distance of at least 400 m and see brilliant coral formations! After this, David and I became good friends. I always visited him and his family whenever I was passing through the greater San Francisco area right up to recent times. We all miss Dave.

8. Stephen Herbert (stephen.herbert@georgetown.edu)

I first connected with Dave Fork when I was a graduate student at the University of Washington working under J. Robert Waaland. Dave and colleagues had published studies of photoinhibition and state transitions, some with the red alga *Porphyra* (Satoh and Fork 1982, 1983c). My interest was in how intertidal species of *Porphyra* survived desiccation and intense sun at low tide while subtidal species died in minutes under the same conditions. I contacted Dave by telephone (a letter may have been sent beforehand but there was no e-mail then) and he graciously invited me to visit and do a few experiments. Scientific hospitality was one of Dave's defining strengths. Over the next 8 years, I made three visits to Dave's lab as a graduate student and continued with him for my postdoc.

Working in Dave's lab was always a pleasure. Most of his capability was in fluorescence yield and absorption difference spectroscopies, using components old and new that could almost always be reconfigured into something effective. Dave once spent a day making a delayed light emission system from a sophisticated optical chopper (pulsed LEDs were exotic at the time) and a roll of black tape. When Shmuel Malkin came, from Israel, to visit us, we built a modulated photoacoustic system that let us see cyclic electron transfer pathways by their storage of chemical energy,

provoking much discussion about what these pathways accomplished (Herbert et al. 1990; Fork and Herbert 1993b). The larger environment of Dave's lab, the Plant Biology Department of the Carnegie Institution at Stanford, was also wonderful. Brilliantly and compassionately directed by Winslow Briggs (1928–2019) at that time, it attracted scientific visitors of all descriptions from around the world. All were approachable at barbecues, and many had lunch in the shrub-hidden circle of Adirondack chairs where Dave and Winslow and Malcolm Nobs were regulars, as were Dave's postdocs. Looking back, I would argue that many fruitful lines of plant biology and photosynthesis research that continue today began or were nurtured in that setting.

Others have written about Dave's connection with the natural world. I remember him taking me to his special place for collecting subtidal seaweeds (which will remain a secret). Academically, I was raised by phycologists, but I had never encountered such an extraordinary field site. Photosynthesis research is ultimately chemistry but always in a biological context that makes it extraordinary. From his earliest work with Francis Haxo, Dave drew chemical insights from biodiversity. This was also one of his defining strengths and instructive to me. During my time in Dave's lab, we mostly worked with intact photosynthetic tissues. This gave confusing results at times but helped us assume they were real, just too complex to understand at the moment. Interactions between photosynthesis and the environment was also a strong theme in Dave's lab and at Carnegie, which resonates with present awareness of climate change, and the role biology must play to stabilize it in years to come. I learned much from my time with Dave, and he was always patient, a third defining strength. His passing is a sad milestone in my life, but my memories of those days will never fade.

#### 9. Tetsuo Hiyama (thiyama@athena.ocn.ne.jp)

I remember meeting Dave Fork a couple of times before I left Charles F. Kettering Research Lab in Yellow Springs, Ohio where I spent 2 years in Bacon Ke's laboratory (see Govindjee et al. 2021). Before Kettering, I was in Britton Chance's lab, in Philadelphia, from 1967 to 1969, where I learned about photosynthesis for the first time and, there, I had studied under the guidance of Mitsuo Nishimura.

I went to the Carnegie Institution in October 1971, which was right after Norio Murata had left there and had returned to the University of Tokyo (see above for Murata's *Reminiscence*). Norio had recommended me there. As a result, Stacy French invited me as a postdoctoral fellow, and I spent the following 3 years working exclusively with Dave. Those were to me the happiest years in my U.S. life (1971–1973). Dave and I worked almost every day in a tiny dark room in the basement. This room, as Dave told me, used to be

a stock room, which had been converted to a lab by Dave and many visiting scientists from around the world. It may be better to call it a huge photometer rather than a room. It had an actinic 'light source' with color filters, a Bausch & Lomb monochromator with a halogen lamp to be used as a measuring beam, a sample holder with a photomultiplier tube at the end, and electronic gears necessary for powering, and amplifying weak signals, and then a recording system. All including the operator, i.e., Dave (and up to two other persons), were neatly packed in the dark room [see above (Fig. 6) for a 1983 photograph of the room]. A year or so later, Dave and I were able to impress a visiting group of Carnegie executives, and, very soon thereafter, they generously provided us funds for implementing an actinic flash apparatus and high-speed data processing devices. Dave and I went to several venture companies in Silicon Valley to inspect their products. We purchased a signal averager and a high-speed (nanosecond) digitizer (Hiyama and Fork 1973). Dave and I published many papers on the results obtained using this dark room photometer, mostly in Carnegie's yearbook (Fork and Hiyama 1972, 1973; Hiyama and Fork 1972, 1973; Fork et al. 1974).

I left Carnegie in the October of 1973 to Daniel Arnon's lab at UC Berkeley. There, I worked for nearly 5 years. During those Berkeley days, I frequently went back to Carnegie to see Dave, Jan Brown and Stacy French, driving 100 miles round trip from Berkeley to Palo Alto (Stanford). It was fun to meet Dave each time and to discuss our research.

#### *A story involving my time in Dan Arnon's lab*

In 1978, taking vacation this time from UC Berkeley, I went to Dave's lab and stayed for several days working on flash-induced high-speed kinetics of algal particles. I also stayed with his family in his woody Portola Valley home during that time. That was my *underground* study; 'underground' was an in-house slang in Arnon's lab, where I would work on research projects given (dictated) by Dan Arnon every day for work from 10 am to 5 pm. After five, I would start my own experiment. In 1977, Arnon had purchased an EPR apparatus together with a liquid helium cryostat. It took me almost 1 year to operate this system, and finally, I was able to look at Component X as well as Centers A and B, then supposedly a 'true' primary electron acceptor of Photosystem I. I worked for Arnon using this EPR instrument to *prove* Arnon's hypothesis of three photosystem theory, which I did not like at all! My 'underground' study was to find out whether a spectrophotometrically detected Photosystem I acceptor, P430, which I had found and named in Bacon Ke's lab in Ohio in 1971, corresponded to the EPR signals of Centers A and B, and the Component X.

Together with the kinetic data obtained spectrophotometrically at Carnegie, Dave and I concluded that P430 is neither the Center A nor the Center B, but it is Component



X. This paper was presented first at the Annual Plant Physiology Conference in Columbus, Ohio, in the summer of 1979; the full paper was published in 1980, after I went back to Japan (Hiyama and Fork 1980). I believe that Arnon knew my *underground* work but, generously, never said anything to me. We had very good relationship.

I met Dave and his family again in 1987, when they came to Japan on a sabbatical leave of absence from Carnegie. Our family picked them up at Haneda Airport, Tokyo. Our newly bought wagon-type car was big enough for Dave, Jody and their three daughters plus my family members—my wife and two baby daughters. I drove the car to the central Tokyo. On the way, I remember, Dave noticed a traffic sign, “Atsugi”, that, he said, was the name of a US military base where he was stationed right after the World War II. I parked the car in a municipal parking lot near the Imperial Palace. There, we had a nice picnic. Then, I took them to Ginza Street, where they were delighted to walk around. On the same day, the Fork family left Tokyo for Kanazawa to see Satoshi Hoshina and then to Okazaki, to join the laboratory of Norio Murata (see his *Reminiscences*).

Right after the Fork family visited Tokyo, I took a short sabbatical and went to SERI (Sustainable Energy Research Institute) in Golden, Colorado with my family. We stayed there for three months. In October, we visited, on our way home, Dave and his family, this time in their Woodside home, and stayed with the family for a couple of wonderful days in this woody and beautiful environment. All of this was in 1987. Since then, I had not had a chance to see Dave and his family. When Govindjee and Norio told me of Dave’s passing at the age of 91, I was astonished, and, then I realized my own age, soon to be 84. I am now reminiscing how great David Fork was not only as a scientist, but also as the warmest human being, and a great friend to all (see a photograph of mine with Dave in the Supplementary Material). We all miss Dave.

#### 10. Joseph Berry (jberry@carnegiescience.edu)

So many memories flood into my mind when reading these tributes. Dave’s time at Carnegie was a very special one. Science has now become more intense, competitive and perhaps more lonely since Dave retired. He presided over a time of relaxed exploration of the mechanisms of photosynthesis and of great creativity. Dave took me “under his wing” upon my arrival as a postdoc few years after his own. He guided me in studies of the effect of temperature on photosynthesis. While we seldom worked together, we often talked about ideas and new developments in the field of photosynthesis. I benefited greatly from Dave and the illustrious train of visitors who came to work with him—some of whom have contributed to this memoir. Dave was also a very helpful and fun colleague who made the Department



**Fig. 12** Left to right: Josh, Luisa, and Alexander Peterson; Laurie Fork Peterson; and Dave Fork, Woodside, California, 2015; Photo by Rajni Govindjee

of Plant Biology a great place to work. As an example, I think of the Carnegie cabin located in Inverness near the Pt. Reyes Natl. Sea Shore. When I arrived in 1970, Dave and several others from the lab were putting finishing touches on this “A-frame” cabin with a beautiful view overlooking Tomales Bay. The facility was funded with a bequest from Vannevar Bush, a past President of the Institution who wrote that, *scientists don’t take enough time for recreation*. Dave played a major role in proposing the project, finding its site, and in the construction of the cabin. This facility has for 50 years lived up to Vannevar Bush’s vision—with nearly constant use by Carnegie staff, students, and visitors for a nominal fee. This facility, which was Dave’s vision, has been a major “perk” that made Carnegie an even better place to work. When I think of Dave, I think of all the joy that the Inverness cabin has brought to our community of scientists, their friends and family over all of these years. Dave was a great scientist and a wonderful human being. He will be missed, but he has left a wonderful legacy.

We end this section of “[Reminiscences](#)” with a wonderful photograph of David when Laurie and her family were visiting him at his home in Woodside, California (Fig. 12). Govindjee and his wife Rajni were also visiting him at that time and had a great time with Dave; they both miss him greatly. See Supplementary material for additional photographs in Dave’s memory.

Dave is survived by his daughters, Laurie Fork Peterson (coauthor of this Tribute), Patricia Orlando and Susanne Fork, and their families including his five grandchildren—Alexander, Luisa, Phoebe, Ginger, and Rune.

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## Declarations

**Conflict of interest** All the authors declare that there are no conflicts of interest.

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## Supplementary Material

for

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### **David (Dave) Charles Fork (1929-2020): A gentle human being, a great experimenter, and a passionate researcher**

by

Govindjee Govindjee, Laurie Fork Peterson, Kazuhiko Satoh, Stephen Herbert, Yaroslav de Kouchkovsky, Ulrich Schreiber, Norio Murata, Gunnar Öquist, Anthony W. D. Larkum , and Joseph A. Berry

Contact e-mails for the Supplementary Material are: [gov@illinois.edu](mailto:gov@illinois.edu) (Govindjee) and [lauriefork@yahoo.com](mailto:lauriefork@yahoo.com) (Laurie Fork)

Here, we present a *Reminiscence* from Guy Samson (Département des sciences de l'environnement, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières, QC G9A 5H7, Canada), followed by several photographs of David (Dave) Fork from his early days till his later years.

#### **1. Reminiscence by Guy Samson (e-mail: [guy.samson@uqtr.ca](mailto:guy.samson@uqtr.ca))**

When I started my Ph.D. in 1986 under the supervision of the late Prof. Radovan Popovic, among my first readings in the field of photosynthesis was a review by David Fork and Kazuhiko Satoh on the '*state transitions*', published in the Annual Review of Plant Physiology (37:335-361). That review impressed me by its clarity, so that the concepts like '*spillover*' and '*absorption cross-section*' were understandable for the newcomers like me. At that time, I learned also much about chlorophyll fluorescence transient (the Kautsky effect) in the 1986 book "Light Emission by Plants and Bacteria", edited by Govindjee, Jan Amesz and David Fork. Thus, at the beginning of my Ph.D. studies, David Fork was for me a big name from the big league.

I first met David Fork in July of 1988 at the C. Stacy French Symposium on Photosynthesis held in Stanford, California. I was highly impressed with him when I discussed, in my broken English, my results during the poster session. My first impression of David was a cheerful, friendly, and energetic person, readily riding his bike. So, the big name became Dave Fork.

In 1989, I received a postdoctoral fellowship from NSERC (Natural Sciences and Engineering Research Council) of Canada, thanks to Dave's support with his nice letter ending with "having good and productive time at Carnegie". This wish became a reality! Two days after my doctoral defense, I embarked on a 5000-km road trip, from my hometown Shawinigan, in Québec, to Palo Alto, California. I still have this vivid memory of Dave's warm welcome, when I



reached Carnegie: he descended the hallway from his office to the front desk, with a large smile, his brilliant eyes and his hand reaching toward me! He knew how to make you feel at ease. He encouraged me to pursue my interest that I had developed near the end of my Ph.D. research on the *enigmatic* cytochrome *b559*; I worked in the basement of the Carnegie building with a dual-wavelength Perkin-Elmer Hitachi 356 spectrophotometer, old but reliable (except for the chart recorder and its leaky ink-pencil!). Dave also offered me the opportunity to collaborate on projects with my sympathetic fellow postdoc Steve Herbert, and with the late David Laudenback from Arthur Grossman's lab, studying the process of photodamage and the acclimation to growth irradiance in a mutant strain of *Synechococcus* lacking iron superoxide dismutase. I learned also much by contributing to a study with Prof. Harry Smith, visiting from the University of Leicester, to assess the roles of phytochromes in photosynthetic acclimation to natural shade.

The success of these different projects is due in large part to the nice ambiance around Dave, which I describe as both stimulating and relaxing at the same time. Steve, Dave, and I had our *lab meetings* twice a day, around 10 am and 3 pm, drinking tea (a habit that I continue) and discussing science, among other topics! In these meetings, Dave always had homemade cookies or cakes. So pleasant and productive times indeed!

Thirty-five years later after leaving Carnegie, I could easily make a list of the scientific and technical knowledge I learned from Dave. But the most important thing I gained from him is invaluable: it is his strength of kindness, of generosity, of words of encouragement to students and junior scientists. Dave Fork, from a big name was a great man. We all miss him.

## 2. Selected photographs of David C. Fork

**Figures S1 – S4** show four photographs of David at various stages of his life: **Fig. S1** - with his parents and sister in Ohio, USA (1935); **Fig. S2** -- when he was on a plant collection trip in Mexico, under the mentorship of E. Yale Dawson (1943); **Fig. S3** – at Mount Fuji in Japan when he was there serving as an Officer of the US Navy (~1953); and, **Fig. S4** -- at his desk when he was doing research in the Laboratoire de Photosynthèse, Gif-sur-Yvette, France (1962). **Figure S5** shows a portrait of David Fork extracted from a 1977 group photograph of the members of the Department of Plant Biology of the Carnegie Institution of Washington (see Fig. 5 in the main paper). **Figures S6- S8** show Dave with his research colleagues: **Fig. S6** is with Tetsuo Hiyama (of Japan) and Govindjee (of USA); **Fig. S7** is with Anthony (Tony) W.D. Larkum ( of Australia); **Fig. S8** is with the Late Joop H.C. Goedheer (of the Biophysical Research Group at the University of Utrecht, Utrecht, The Netherlands). Finally, **Figure S9** is one of the last photographs he had with Govindjee, his friend since the early 1960s.



**Fig. S1** A young David with his parents, Charles and Emma, and sister, Kathrine, in Ohio, ~1935. Source: The Fork family



**Fig. S2** David as a teenager on a botanical collection trip, examining a giant cardon cactus (*Pachycereus pringlei*) in Baja California, Mexico, 1943. Source: The Fork family

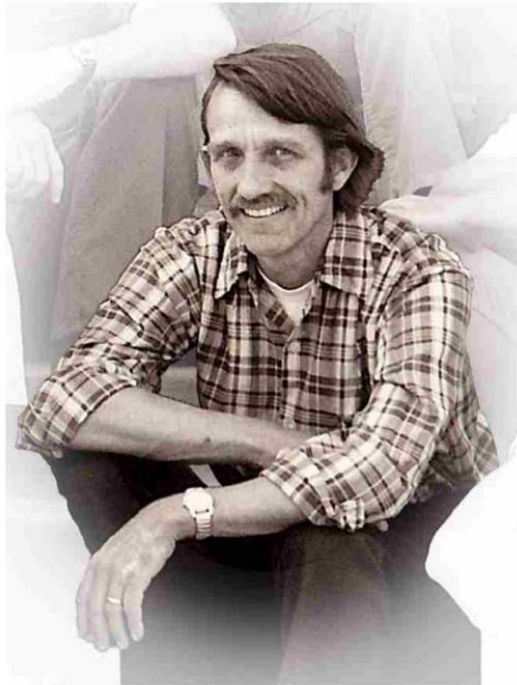




**Fig. S3** David at the top of Mt. Fuji, Japan – 1953. Source: The Fork family



**Fig. S4** David at his desk when he was working as a Visiting Research Investigator at the Laboratoire de Photosynthèse , Gif-sur- Yvette, France , 1962. Source: The Fork family



**Fig. S5** A 1977 portrait of David Fork (see Figure 5 in the main paper). Source: Thomas Uebele of the University of Illinois at Urbana-Champaign





**Fig. S6** David Fork with Govindjee (on his right) and Tetsuo Hiyama (on his left) at the 8<sup>th</sup> International Congress on Photosynthesis, Stockholm, 1989 (see the *Reminiscence* of Hiyama in the main paper). Source: The Fork family



**Fig. S 7** *Left panel:* Tony Larkum and David Fork (hidden behind his video camera) on a trip to examine the flora in Ku-ring-gai Chase National Park, New South Wales, Australia, 1986; *Middle panel:* A scene at the Lizard Island, Great Barrier Reef; *Right panel :* David Fork (carrying his file folder with his notes) at the University of Sydney, Sydney, New South Wales, 1986. Source: The Fork family



**Fig. S8** A 1989 group photograph in Amsterdam, The Netherlands. **Left to right:** Jody Fork , Patty Fork, David Fork, Joop H.C. Goedheer, and Susie Fork. Source: The Fork family





**Fig.S9** David Fork and Govindjee Govindjee (both smiling and enjoying the stories of their life-long photosynthesis research) at 30 Summit Road, Woodside, California, during their last meeting in 2016. Photo by Rajni Govindjee