



Remembering Robert (Bob) Togasaki (1932–2019): A leader in *Chlamydomonas* genetics and in plant biology, as well as a teacher par excellence

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Abstract

Robert (Bob) K. Togasaki was devoted to science and the people in the scientific community. He elucidated some of the most fundamental aspects of photosynthesis and carbon metabolism through classic genetic approaches and later using the tools of modern biotechnology. Along the way, he freely shared his ideas and enthusiasm with established scientists, junior researchers, graduate students, and even elementary students. His career trajectory led him to work with some of the leaders in the field, including the late Martin Gibbs and R. Paul Levine. His dedicated research has led to a more complete understanding of some of the core biochemical functions relating to photosynthesis of the green alga *Chlamydomonas*; this has included carbon-concentrating mechanisms, hydrogenases, and superoxide dismutase to name just a few. The focus of this Tribute is personal reminiscences by his postdoctoral advisor R. Paul Levine; his collaborators Teruo Ogawa, Jean-David Rochaix, Hidehiro Sakurai, Michael Seibert; and by his students William Belknap, Susan Carlson, Charlene Forest, Arthur Grossman, Gregory Katzman, Masahiko Kitayama, and Jon Suzuki. All remember Bob Togasaki for his intellect, dedication to science education, and his unwavering goodwill and optimism towards his fellow human beings.

Keywords Carbonic anhydrase · *Chlamydomonas* genetics · Bionebulizer · Arthur Grossman · Martin Gibbs · Paul Levine · Stefan Surzycki

Early life

Robert (Bob) Kiyoshi Togasaki, born on July 24, 1932, in San Francisco, California, died on November 19, 2019, in Bloomington, Indiana. His father was George Kiyoshi and

his mother Misu Kanamori Togasaki. To begin with and before saying anything more about Bob, we show three photographs of Bob—in both formal and informal settings (Fig. 1).

When Bob was only a year old, the family moved to Japan. His father was born in the USA, but his mother was born in Japan. During the 1930s, she was required to make frequent trips back to Japan to fulfill certain immigration requirements. Rather than subject the family to the long-distance travel, the family moved to Japan. Life during World War (WW) II (1939–1945) could not have been easy for them (see *Reminiscences* by William Belknap). Although Bob did not speak much of those years, he did recount that following WWII, his father rose to prominence in Japanese business circles, as he was one of the few bilingual Japanese citizens. Consequently, Bob's father was called in for many negotiations with the US Government (as an aside, we note that in 1968, Bob's father became the first Japanese president of Rotary International). Growing up in Tokyo, Bob attended Shakujii Elementary School and then Gakushuin School. It was at Gakushuin that Bob met the future Japanese

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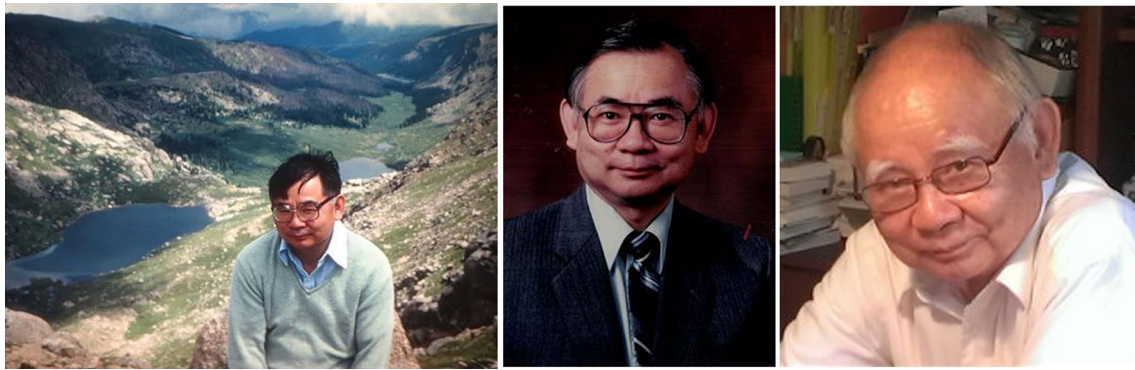


Fig. 1 Left to right: Three photographs of Robert Togasaki: from the 1980s (Colorado; provided by Kenneth Spencer), the 1990s (Indiana), and the 2000s (Indiana), the latter two from the Archives of Indiana University



Fig. 2 Left to right: Elizabeth Gray Vining, the Japanese Crown Prince Akihito (later Emperor) and Robert Togasaki. Photo taken in 1953; for details and source, see Lotozo (2017) and Sachs (2019)

Emperor Akihito. Due to Bob's proficiency in English, he was among a select group of students participating in private tutorials with the Crown Prince Akihito. The two classmates became lifelong friends (<https://haver.blog/2017/05/22/history-lesson-the-japanese-emperors-visit-to-haverford/>, <https://www.baltimoresun.com/opinion/op-ed/bs-ed-op-0520-akihi-to-meeting-20190517-story.html>, and, Lotozo 2017; Sachs 2019). See Fig. 2 for a 1953 photograph of Bob with the Crown Prince, and their common tutor Elizabeth Gray Vining. Bob returned to the U.S. in 1949, where he studied first at the famous Phillips Exeter Academy (Exeter, New Hampshire; <https://www.exeter.edu/>) and then at Haverford College (Haverford, Pennsylvania; <https://www.haverford.edu/>), where he received a B.S. in chemistry in 1956. Three years later, he married his long-time friend Fumiko Tomoyama, now deceased (1932–2014). Bob always felt a bit embarrassed by his graduation from the prestigious Phillips Exeter Academy, a school known for educating children from elite

U.S. families. He explained that at the time, the school was seeking to diversify its student body and Bob, as a U.S. citizen, was “easy” to recruit.

Graduate school, postdoctoral days, and early research

Robert Togasaki obtained his Ph.D. in Biochemistry in 1964 from Cornell University in Ithaca, NY, working with the world-famous photosynthesis expert Martin Gibbs (1922–2006; see Gibbs 1999; and, ASPB News 2006). The title of his thesis was “Enhanced dark $^{14}\text{CO}_2$ fixation by preilluminated algae,” where he explored the role of a postulated light-generated reductant in the assimilation of CO_2 through the “light independent reactions” of the reductive pentose phosphate pathway (Togasaki and Gibbs 1963, 1967). Bob was very appreciative of Professor Gibbs and wrote a wonderful tribute to him upon his death (see ASPB News 2006; and, <https://aspb.org/newsletter/archive/2006/septoct06.pdf>). In 1964, Bob joined Harvard University, Cambridge, MA, where he did his postdoctoral work with a top authority in genetics, Paul Levine. It was in his lab that Bob first utilized mutants of the green alga *Chlamydomonas reinhardtii* to explore photosynthesis and, specifically, RuBP carboxylase/oxygenase (Rubsico, then known as RuDP carboxylase). Levine and Togasaki (1965) described the first mutant ever identified that lacked Rubisco. This seminal work on the most important enzyme of photosynthesis was key to establishing Bob as a world leader in photosynthesis research. While Bob was not a geneticist per se, he quickly established himself as a top plant (and algal) biologist who had a knack for designing screens and selections of mutants, and then with his deep understanding of biochemistry, he unraveled specific biochemical pathways (see e.g., Goodenough et al. 1971, Togasaki and Whitmarsh 1986, and

Togasaki and Surzycki 1998). It was at Harvard where Bob met his good friend, and later fellow Indiana University faculty member, Stefan Surzycki.

Research and teaching

In 1968, Bob joined the faculty of the Botany Department (later Biology Department), at Indiana University (IU), Bloomington, Indiana. His research interest complemented and strengthened the department's emphasis on the biochemistry of photosynthesis (Belknap and Togasaki 1981a); other notable IU professors in this area were Anthony (Tony) San Pietro (1922–2008) and Howard Gest (1921–2012). For Togasaki's research on this topic, see: Palmer and Togasaki 1971, Togasaki and Hudock 1972, Lien et al. 1974, Brand et al. 1975, Curtis et al. 1975, Hudock et al. 1979, and Murota et al. 2012. He was promoted to full professorship in 1983, retiring in 1997 after 30 years of outstanding service. During his stint at IU, Bob spent sabbatical time at three major research centers: (i) University of Tokyo (Institute of Microbiology), (ii) Carnegie Institution of Washington at Stanford, California, and (iii) at RIKEN (Institute of Physical Chemistry Research) in Wako-Shi, Saitama, Japan.

While Bob's research interests were focused on photosynthesis and related biochemical reactions, he was innately curious and creative as a researcher (see e.g., Togasaki and Botos 1971, and Sakata et al. 1997). One of his earliest Ph.D. students, Charlene Forest, studied gametogenesis in *Chlamydomonas*. While this seemed to be outside of Bob's expertise, they designed a selection procedure making use of the *pet-10-1* photosynthetic electron transport mutant and methyl viologen to isolate temperature sensitive gametogenic mutants (See [Reminiscences](#) by Charlene Forest; and Forest and Togasaki 1975, 1977).

Bob's research interests during the late 1970s into the 1980s continued in the area that he was already an expert on: the biochemistry and genetics of *Chlamydomonas*. He exploited this single-celled green alga to the utmost level by making and using novel mutants, thus, further elucidating our understanding of photosynthesis (see e.g., McBride et al. 1976, and Spencer and Togasaki 1981). One of his interests during this period involved the O₂ sensitivity of hydrogenase (the enzyme that releases molecular H₂ gas). If algae were ever going to be used to generate H₂ as a renewable form of energy, this limitation would need to be dealt with. Bob and others (see e.g., McBride et al. 1977) isolated hydrogenase mutants, less sensitive to O₂. Michael (Mike) Seibert's lab carried this work forward; he credits his collaboration with Bob for the isolation of additional mutants and further understanding of this enzyme (see [Reminiscences](#) by Mike Seibert; and Ghirardi et al. 1997).

Also in the 1980s, Jean-David Rochaix recalls a wonderful collaboration with Bob to probe the structure–function relationship of the reaction center protein D1 of Photosystem II (PSII) using herbicide-resistant *Chlamydomonas* mutants (see [Reminiscences](#) by J-D Rochaix; and Erickson et al. 1989).

In addition to the above, Bob Togasaki probed, in detail, the role of superoxide dismutase and a few other enzymes (see e.g., [Reminiscences](#) by Hidehiro Sakurai, de Hostos et al. 1988, M. Kitayama and Togasaki 1992, K. Kitayama and Togasaki 1993, Sakurai et al. 1993, M. Kitayama et al. 1994, K. Kitayama et al. 1998a, and K. Kitayama et al. 1999). However, during the final years of his research life, he returned to work on carbon metabolism and focused on understanding the carbon-concentrating mechanisms (CCM) in *Chlamydomonas*. Of particular importance to this area of interest was the detailed study of the key function of carbonic anhydrase (CA). Carbonic anhydrases are ubiquitous to both photosynthetic and non-photosynthetic organisms, catalyzing the inter-conversion of CO₂ and bicarbonate (see e.g., Badger and Price 1994, and Moroney et al. 2001). This became an active area of research (see e.g., Coleman et al. 1984, 1985). Bob turned to the isolation of mutants that were key to understanding the mechanism of inorganic carbon uptake. In another example of Bob's creativity, using everyday materials, he designed a method for isolating high CO₂ requiring mutants using duct-taped sealed clear plastic boxes, and solutions of water saturated with NaHCO₃ to generate CO₂ (see Coleman et al. 1985). Using this method, Bob and his collaborators and students would go on to establish the location and the characteristics of several different carbonic anhydrases from *Chlamydomonas* cells grown under different growth regimes (for different aspects, see Kimpel et al. 1983; Spencer et al. 1983; Moroney et al., 1987a, b, 1989; Husic et al. 1989; Katzman et al. 1994; Sasaki et al. 1997; and [Reminiscences](#) by Arthur Grossman). Bob even designed a new method for assaying carbonic anhydrase using *Chlamydomonas* cells as a remarkably efficient ¹⁴CO₂ trap (see [Reminiscences](#) by Gregory Katzman; and Katzman et al. 1994).

Almost a dozen PhD students (including Charlene Forest, Arthur Grossman, Ken Spencer, William (Bill) Belknap, Masahiko and Kaoru Kitayama, and Susan Carlson, one of the authors of this Tribute) finished under Robert Togasaki's wonderful and friendly guidance (see the section on [Reminiscences](#), by several scientists, for personal and detailed picture of Bob Togasaki).

Most of us have been highly impressed with the major contribution of Bob Togasaki in the development of what was originally called the “Bionebulizer” (see Okpodu et al. 1994; also see Degouys et al. 1997). In 1993, it was listed as one of the 100 discoveries of the year by Research and Development Magazine. Working with the designer of the

device and fellow IU professor, Stefan Surzycki, and with Masahiko Kitayama, the device called “Bioneb” was patented (“Process and apparatus for fragmenting biomaterials”; patent #5,506,100; April 9, 1996 by S. Surzycki, R.K. Togasaki and M. Kitayama; and patent #5,610,010; March 11, 1997 by Surzycki, Kitayama and Togasaki; patents are accessible at <https://www.uspto.gov>). The “Bioneb” has been used by many around the world since it is used to make “intact” chloroplasts for research on photosynthesis outside the cells as well as other plant cell fractionation applications! (See Michael Seibert’s *Reminiscences*; and Belknap 1983, Togasaki et al. 1987, as well as Togasaki and Surzycki 2000).

In addition to research, Bob was a beloved teacher at IU, as noted by both graduate students and undergraduates. He was the “Super Teacher” for “Cell Biology,” and for an undergraduate cell biology lab where the emphasis was on basic concepts, not just routine techniques. Not surprisingly, three out of the 16 laboratory sessions were on photosynthesis; one even used *Chlamydomonas* mutants. Bob had the good fortune to have his long-time friend, Judy Surzycki manage the Cell Biology laboratory course. His enthusiasm for teaching science would carry over into his retirement (see below).

Extra-curricular teaching and devotion to science and people

Bob Togasaki loved not only plant biology, but also all the people that he associated with. He was a volunteer teacher at Harmony School in Bloomington (a private elementary through high school), and he also taught Biology at WonderLab, a science museum for children (<https://www.wonderlab.org/>), where, we are told, he loved spending time teaching the thrill of science to young children. Figure 3 shows Bob with the kids he loved to teach, as well as a cookie—made to represent the green alga *Chlamydomonas* that he loved to work with.

Bob Togasaki not only cared for the young, but for the seniors in the community; he served on the Board of Directors for Area 10 Agency on Aging in Bloomington (<https://area10agency.org/>). Also see further information on Bob Togasaki as well as others at IU: <https://biology.indiana.edu/news-events/newsletters/2020-spr-newsletter/in-memoriam.html>. We also note that he was instrumental in developing the Joan Wood Lecture Series at IU. This lecture series honors the memory of one of Bob’s early students and is designed as a forum for undergraduates to interact with women in science-related careers (see: <https://biology.indiana.edu/news-events/named-lectures/wood-lecture-series.html>).



Fig. 3 Bob Togasaki (Left) explaining to school children how plants grow, and how photosynthesis provides food and energy (Archives of Indiana University), and (Right) holding a “*Chlamydomonas*

(*Chlamy*) cookie” that his lab members had designed and was made by the Indiana University student union’s bakery section (Source: Charlene Forest)

Reminiscences

Carl Bauer (Distinguished Professor, Indiana University, Department of Biology; e-mail: bauer@indiana.edu)

Bob was one of the first faculty members that I interacted with when I joined the IU Biology department in 1988. Soon after my arrival, Bob and I co-taught a graduate class on photosynthesis and plant physiology. I was responsible for teaching the biochemistry and biophysics behind how light energy is captured and converted into cellular energy and Bob took it from there to discuss how this captured energy is used by cells to undertake cellular metabolism (e.g., CO₂ fixation). Bob's physiology lectures really enlightened me on details of chloroplast physiology as I was a trained microbial biochemist and not at all educated in plant physiology. Co-teaching with Bob led to a series of discussions about Bob's research on *Chlamydomonas* and his ability to use biolistics to disrupt chloroplast genes [Sanford 1988; for other examples of Bob's work with cellular devices, see Kitayama 1990 (biolistics) and Okpodu 1994 (BioNeb)]. At the time this was state-of-the-art methodology and really an incredible way to knock out chloroplast genes (Sanford 1988). During this early period, several students in my lab were studying genes involved in the synthesis of bacteriochlorophyll and from this analysis, Jon Suzuki, from my lab, realized that there was a chloroplast homolog to a gene coding for a subunit of dark-operative protochlorophyllide oxidoreductase (DPOR). Bob and his graduate student Masahiko Kitayama graciously taught Jon how to use biolistics to disrupt this gene from the *Chlamydomonas* chloroplast genome leading to a high impact paper in the *Plant Cell* (Suzuki 1992).

In later years, after Bob had closed his lab, he would come to my lab to grow cultures of the purple photosynthetic bacterium *Rhodospirillum rubrum*. This species exhibits robust phototaxis (Ragatz 1995) that can easily be visualized by trapping cells into a small beam of focused light on a cover slip. Bob would use these cells to set up an experiment at our local children's science museum where he delighted children with a microscope that showed how photosynthetic bacteria moved in response to the presence of light.

In thinking back on my interactions with Bob, I recall that he always walked the halls, or came into the lab, with a big cheerful smile. He was also passionate about science education at all levels-graduate-undergraduate and societal with inquisitive kids! Bob's passing is a loss to everyone that was fortunate enough to know him.

William Belknap (Retired, formerly with United States Department of Agriculture-Agriculture Research Service; e-mail: williamrbelknap32@gmail.com)

About Bob's childhood in WWII Japan. One day we were in the growth room, identifying and labeling single isolates in a mutant screen (for photosystem II, as I remember). (For related research, see: Belknap and Togasaki 1981a, Belknap and Togasaki 1981b, Belknap and Togasaki 1982, and Belknap 1983.) I was labeling mine A1 through A100, he was labeling his B1 through B100. While I was putting away the plates, I noticed that all the other isolates were there, but there was no B29. I told him "Hey Bob, you forgot B29." He looked at me with an odd expression and said "No I didn't." I was so embarrassed, in my focus on the task I had forgotten that he grew up with a sky full of B29 Superfortresses dropping incendiary bombs, when he was in Japan. He realized how bad I felt, and he spent about an hour over coffee telling me stories about being a kid in WWII Japan. I believe he did that just to make me feel better.

Bob as a mentor

My favorite Bob story comes from 1988, years after I left the lab. My first year at the USDA/ARS was a little rocky (to say the least, the following 29 years were terrific), resulting in some seriously negative interactions with my immediate administrators. At one point, one of these administrators read me the letter of recommendation that Bob had written for me, telling me he wished he had listened to Bob. I quote part of Bob's letter: *Bill is like a wild horse, he will not always accomplish what you expect, but he will always accomplish something.* "A wild horse, what a thing to write in support of a candidate for a government job. Totally true, but wow! This brief story clearly illustrates my favorite of Bob Togasaki's many wonderful attributes: his complete and unflinching honesty. *Perhaps the most straightforward human I ever met.* I cannot imagine another lab where I could have successfully completed graduate school. It was his intelligence, generosity and kindness that allowed me to have a career that was more fun than probably should have been allowed. For that I will be forever indebted to him.

Susan J. Carlson* (U.S. Food and Drug Administration (FDA); e-mail: susiecarlson@verizon.net)

I was a Ph.D. student in Robert Togasaki's Lab, and I graduated in 1995 (dissertation title: Purification and characterization of the chloroplastic carbonic anhydrase from *Chlamydomonas reinhardtii*). I owe much to the training and experiences I had working and watching my teacher, who I would call Bob in my *reminiscences*. I have so many wonderful memories of my time with him. He was a fine

scientist who contributed much to the field of photosynthesis and *Chlamydomonas* research. Those accomplishments speak for themselves through his list of publications, some of which are briefly mentioned above. While Bob would blush at all of this attention, I think he would smile quietly and accept the recognition of himself as a great mentor and teacher. More than anything, Bob believed passionately in mentoring the next generation of scientists, especially those from communities under-represented in science. I suspect that this passion was rooted in Bob's own humble background (see above for Bob's early life). Bob often spoke to me about how his life's trajectory was positively influenced through the help and kindness of others, even though he was an "outsider." Bob wanted me, and all of the students he interacted with, to find our way to happiness and success, and he would do anything he could to help. I'm sure that every one of Bob's mentees, formal and informal, carry Bob's mission in their hearts and do their part to pay it forward. I am so grateful to have had Bob in my life.

Bob the mentor

One of the many recipients of Bob's mentoring was the undergraduate dishwasher/media maker for the lab. This young, African-American woman came from modest means and was a first-generation college student. Bob quickly became her greatest fan. Not only did he encourage and guide her through her academic pursuits, but he also arranged for Anthony (Tony) San Pietro (1922–2008; US National Academy of Science (NAS) member and then a retired faculty) to be her chemistry tutor. The two of them became fast friends and had many chemistry tutoring sessions. When the young woman joined one of the African-American service-oriented sororities at Indiana University, Bob was all in! He loved that she wanted to give back to others and he helped her out on some of her projects. Bob and Tony would be so proud of their mentee—she went on to earn her Ph.D. and is an epidemiologist with the Centers for Disease Control (CDC).

Bob as a humble man

Few things bothered Bob more than pretense. When he and fellow BioNeb collaborators won an award for the Bio Neb, he was told that the award ceremony required him wearing black attire. He was in a bit of a panic over this. He had one disheveled sport coat that hung in his office for emergency purposes. He saw no need for getting dressed up. The organizers told him that it would be ok if he showed up in a sport coat and tie, but even this upset Bob. He saw getting dressed up as a pretense...something he did not want any part of. I advised him to think about it as just showing respect to other people. Later, when it was time for me to graduate, I convinced Bob to go through the ceremony with me. Knowing that he did not like to get dressed up, I had to figure out a way to talk him into it. I talked it up



Fig. 4 Susan Carlson (one of the authors) with her Professor Robert Togasaki in their academic gowns at Carlson's 1995 PhD graduation. Source: Susan Carlson

as an interesting experience. I do not believe he had ever been to any graduation, maybe not even his own. As I was his last Ph.D. student, this would be the final opportunity. Bob kindly agreed and we both got decked out in the caps, gowns, and hoods. Bob and I sat together on a beautiful spring day in Bloomington, and he placed the hood over my head. It was a big event for both of us and one that I will always remember. My dear friend, Betsy Whitehead, hosted a lunch at her home for just Bob and me after the graduation. Betsy also took a picture of us that I cherish (Fig. 4).

Charlene L. Forest (Professor Emerita, Brooklyn College of City University of New York; e-mail: drclforest@gmail.com)

It seems that everyone who knew Bob had the same impression: that he was one of the most caring individuals they had ever met. He was also one of the most creative people I have had the pleasure of working with. Bob had endless energy and was always happy to sit down with us and help us come up with and analyze research ideas. As a grad student, when I was looking for a research topic, I spoke to Bob, who gave me an idea he had about creating mutants

of *Chlamydomonas* that were unable to mate. His selection procedure was ingenious. I found his ideas so interesting, that they became the basis of my thesis and my entire career. This was not his area of research and in fact as far as I know, I was the only non-photosynthesis person to work in his lab.

At one time, Bob was helping me with an experiment where we needed to add a reagent to several tubes at a specific time, so Bob was counting down for me. Suddenly, I realized that I could no longer understand what he was saying—so I exclaimed ‘Bob count in English, I don’t understand Japanese.’ It all worked out fine, and we published two important papers on conditional gametogenesis in Bob’s favorite green alga *Chlamydomonas* (see Forest and Togasaki 1975, 1977). Figure 5 shows two photographs of Bob with me.



Fig. 5 Top: Charlene Forest and Robert Togasaki at the “Chlamy 1998” meeting (the 8th International Conference on Chlamydomonas, held in Tahoe City, June 2–7, 1998). Bottom: Left to right: Steve Yarris (Charlene Forest’s husband), Charlene Forest, Robert Togasaki, and her graduate student Munevver Aksoy, at the “Chlamy 2006” meeting (the 12th International Conference on the Cell and Molecular Biology of Chlamydomonas, held in Portland, Oregon, May 9–14, 2006)

Arthur Grossman (The Carnegie Institution for Science, Stanford, CA, Department of Plant Biology; e-mail: arthurg@stanford.edu)

I received my PhD, in 1978, working with Bob Togasaki at Indiana University (Bloomington, IN), and had a wonderful time with him over the years discussing science, people and his own life and difficulties. He was a strong mentor; I studied a variety of photosynthesis mutants of the green alga *Chlamydomonas reinhardtii* when I was in his Lab (see Grossman 1978; cf. Grossman 2000). We continued to work together even after I went to the Carnegie Institution for Science (at Stanford, CA), where we published on carbonic anhydrase in *Chlamydomonas* (Coleman et al. 1984, 1985; see also de Hostos 1988). While Bob enjoyed the university life and the American culture, he did often harken back to his friends (some of royal blood... up to the emperor, and his wife; Fig. 1) and family in Japan. There were also many times that we would get together and discuss the academic lifestyle and the ways in which it enriches individuals through common interests, common acquaintance, travel to unique and exciting places, meeting new and fascinating people (people who think differently), both at conferences and when visiting other universities.

Bob visited us in California several times, where he stayed with me and my wife, Devaki Bhaya, especially during his trips to Japan. His health was strongly impacted when his wife, Fumiko, began to suffer from dementia and ultimately passed away. During that period Bob talked to me quite a bit about being retired and finding a new meaning in teaching in the Indiana public school system and trying to excite the students, and with his work for a small science museum. He seemed to enjoy those roles, at least for a while. As time



Fig. 6 A photograph of a painting by Harry Engel (1901–1968), a Romanian artist, who was at Indiana University; the painting was given, as a gift, to Arthur Grossman by Robert Togasaki. Source: Arthur Grossman

went on, we stayed in contact but not as much, and Bob was being targeted by con artists who promised him great financial benefits if he just sent them \$100, \$200, \$500... he seemed to get more and more trusting as he got older and older. He wanted to believe in people. I have various gifts that Bob gave me over the years (he was very generous), but there is one special gift that I cherish, which is a painting by Harry Engel (1901–1968), a Romanian artist, who was at Indiana University. This painting, which hangs in my living room, is a picture of an anguished woman peering at several birds, right-side up, up-side down, singing, eating, thinking, squawking, and maybe even collapsing (I am sharing this painting with everyone; see Fig. 6). It is the complexity of this picture that reminds me of the humanism and complexity of Bob, aspects of his character I benefited from greatly. And to this day I feel a little foolish and guilty for not taking a little more time to appreciate and explore that complexity during his last years.

Gregory Katzman (MD, MBA, FACR; Service Chief, Radiology, Richard L. Roudebush VA Medical Center, and Professor of Radiology & Imaging Sciences, Indiana University School of Medicine; e-mail: gkatzman@mindspring.com)

I remember working side-by-side with Bob Togasaki in the lab creating a crazy contraption with a shaking platform, growth lights, injecting radioactivity, with Chl_a on discs, as a new way to capture carbonic anhydrase activity with high sensitivity. And I'll be damned if it didn't work. This was a great example of his incredible creativity. From this work, we published an important paper comparing carbonic anhydrase activity in chloroplasts from wild type and high CO₂-dependent mutants of the green alga *Chlamydomonas* (see Katzman et al. 1994; see also Aoki et al. 1981). I remember typing my thesis on his computer (Mac) that had the little screen, as it was the only computer platform that could display Japanese, and I couldn't see the whole page at any time. And I remember him being the most thoughtful and caring person I think I've ever met. I had some real personal issues at that time, and he listened to all of them, and the key is that he wanted to do so, not that he thought he should as just an obligation. His understanding and empathic capabilities were immense and seemingly infinite. Although I didn't think at that time that I contributed much to his research interests, and he probably would have been far better off with a different graduate student than me, he supported me at every step of the way, including my transition away from benchtop science to medical school. In 2011, I took Bob to dinner during a visit to Bloomington. He was very honestly thrilled with my academic and clinical successes, even though they were quite a significant departure

from the original path that he and I walked together. Just an amazing man. I tear up as I type this.

Masahiko Kitayama (International Pacific Institute of Indiana Life Science, Inc. and Indiana Global Learning Center; e-mail: masa75@me.com)

I still remember my first flight to the United States on August 19th in 1985. Dr. Tomoko Nakanishi, who was my boss at that time (currently she is the President of the Hoshi University in Tokyo, Japan), waited for me at the O'Hare airport in Chicago. The next day, we both went to Bloomington, IN to visit Bob Togasaki's home. This was the first time that I met Bob and his wife Fumiko. Bob became my graduate school advisor for my Masters and Ph.D. degrees (see M. Kitayama 1994; M. Kitayama and Togasaki 1995; M. Kitayama et al. 1998b). Bob, Fumiko, and I went to movies often before Fumiko left town to teach East Asian Studies at Wittenberg University, Springfield, Ohio. One day after watching the movie 'The Hunt for Red October,' we went to a local café named Runcible Spoon. Another time, we went to see a movie 'Back to the Future.' After watching the movie, we had a good conversation at his house. I can recall these scenes very well even now.

One day in November 2019, I got a phone call from our common friend telling me of Bob's stroke. I rushed to the hospital. However, he was OK at that time and looked good with his smile even though he did not say anything. A few days later, he made his new journey away from all of us. Although we cannot meet him at the YMCA anymore, I feel his presence around me. His last smile, embedded deeply in my memory, encourages me a lot and he continues to be my supervisor from now just like he used to be!

R. Paul Levine (Professor Emeritus, Stanford University; formerly Professor at Harvard University; e-mail: plevine@stanford.edu)

I first met Bob Togasaki when Martin Gibbs (1922–2006) had invited me to give a seminar at Cornell University. It was at this time that in my lab at Harvard University, we were beginning to generate information about the pathway of the photosynthetic electron transport system using mutant strains of *Chlamydomonas reinhardtii*. After Bob finished his PhD, I invited him to do postdoctoral research in my Lab—where there were already at least ten postdocs and graduate students, and a couple of undergraduates. It was an exciting and highly productive time. Bob in his quiet way slipped into it with ease and during his four years he became the mentor and friend of everyone in the lab. I well remember his quick understanding and appreciation for what each of us was doing and for his insightful comments at lab meetings. He did outstanding research. For example, using a *Chlamydomonas* mutant, Bob provided the clearest

evidence for the key participation of ribulose bis [then called di]-phosphate carboxylase RuBP (then RuDP) in photosynthetic carbon dioxide fixation in vivo—further, he showed that this mutant was totally competent in electron transfer process in its chloroplasts (Levine and Togasaki 1965). Further research on the *ac-20* mutant of *Chlamydomonas* led Bob to provide very detailed and thorough information on both its structure and function, particularly on the synthesis of RuBP carboxylase (Togasaki and Levine 1970).

On a personal note, at a time when I was ill for a few days it was Bob who visited me each day to bring me up to date on what each person was doing.

Teruo Ogawa (Formerly Professor at Bioscience Center, Nagoya University, Japan; e-mail: ogawater@xd6.so-net.ne.jp)

After I retired from Nagoya University in March, 2003, Himadri Pakrasi of Washington University (St. Louis, MO) invited me to join his new research project, where I met Yasuhiro Kashino (now a professor at the University of Hyogo, Japan) and his wife Natsuko, who were then visiting Himadri's lab. During this period, we all attended the Midwest/Southeast Photosynthesis Meeting held at Turkey Run, Indiana. We took this opportunity to visit Bloomington (Indiana) and introduce the wonderful scientist, Robert (Bob) Togasaki, to these young Japanese scientists. They were extremely impressed to talk with Bob, with great enthusiasm, about his volunteer work of teaching biology to young people in the community; I was also impressed with his great service-oriented activity. Bob took us to the home of Anthony (Tony) San Pietro, who was earlier vice president of the Charles F. Kettering Research Laboratory (Ohio) when, during 1968–1970, I was a postdoctoral fellow under Leo P. Vernon (1925–2010). This was the last occasion for me to see Bob, Tony and his wife, Alice. In all likelihood, I had met Bob for the first time, long ago, at a workshop on carbon uptake held in California, where I had presented my work on 'post-illumination CO₂ burst from cyanobacterial cells.' Bob was interested in measuring CO₂ exchange by his favorite *Chlamydomonas* cells and visited me in 1986 when I was working as a senior research scientist at the Institute of Physical and Chemical Research (RIKEN: Rikagaku Kenkyushu, at Wako, Saitama, Japan). Although the experiment on *Chlamydomonas* cells was unsuccessful, we demonstrated that carbonyl sulfide (COS) is a potent inhibitor of inorganic carbon (Ci) uptake by cyanobacterial cells (Ogawa and Togasaki 1988). After Bob left RIKEN, I continued to work on Ci-uptake systems in cyanobacteria and identified two CO₂ uptake systems and two bicarbonate transporters. Now, there was a connection with a former PhD student of Bob: Arthur Grossman (see above for the *Reminiscence* by Grossman). In 1994, I had moved from RIKEN

to Bioscience Center of Nagoya University, and I requested Bob to recommend a good scientist who might be interested in visiting the Bioscience Center to do research. He immediately recommended Arthur Grossman. Arthur visited us in 1999 with his wife, Devaki Bhaya, and their 6-month-old daughter, Iilina. We had very good time with Arthur and his family. I thank Bob for sending them. We all miss Bob not only for his great science, but for his lovely encouragement and teaching others wherever he will meet them.

Jean-David Rochaix (Professor Emeritus, University of Geneva, Geneva, Switzerland, Department of Molecular Biology; e-mail: Jean-David.Rochaix@unige.ch)

When I joined the laboratory of Paul Levine as graduate student at Harvard at the end of the 1960s, Bob Togasaki had already left Harvard to take up a faculty position at Indiana University (Bloomington, IN). I heard only good things about Togasaki and how smart he was. It was only several years later that I met him for the first time. He struck me immediately as a very friendly person who put everybody at ease with a creative mind and a deep knowledge of photosynthesis. I had the pleasure to collaborate with him in the late 1980s when we were using herbicide-resistant mutants of the green alga *Chlamydomonas* to analyze the structure-function relationship of the reaction center protein D1 of photosystem II (PSII). This work allowed us to correlate the presence of specific amino acid substitutions in D1 with herbicide resistance patterns and with the rate of electron transfer from Q_A (a plastoquinone bound on the D2 protein) to Q_B (a second plastoquinone bound on D1); we published it in *Plant Cell* (Erickson et al. 1989). I met Bob on several occasions later at meetings and at Indiana University, and I was always impressed with his stimulating ideas, his thoughtful advice, and, above all, his generous help.

Hidehiro Sakurai (Emeritus Professor, Waseda University, Japan; e-mail: sakurai@waseda.jp)

I am very happy to be given this opportunity to participate in writing a tribute to Dr. Robert Kiyoshi Togasaki. He was a very warm-hearted person, with full of humor. I visited his laboratory for a half year in 1991, and wrote a paper with him on Fe-super oxide dismutase (SOD) from the green alga *Chlamydomonas*, his favorite organism (Sakurai et al. 1993). Among the graduate students at Indiana University that I remember, we had Arthur Grossman (now at Carnegie Institution of Washington; see his *Reminiscence*), and Susan J. Carlson (now at U.S. Food and Drug Administration; see her *Reminiscence*). I marveled the fact that Togasaki was not only superb in research and teaching but was concerned with helping the less privileged in the society. I remember seeing

him mentoring, with great dedication, an African American student for her to develop her own independent career. Further, I also appreciated that he actively participated in the local community in Bloomington Children's Science Museum; all of this reflects on his care and concern of ALL the people—both young and old, and, men and women (see above for Figure 3 of Bob with students).

Michael Seibert (Research Fellow Emeritus of the National Renewable Energy Laboratory (NREL) and Research Professor, Colorado School of Mines, Golden, Department of Environmental Science and Engineering; e-mail: Mike.Seibert@nrel.gov)

The O₂ sensitivity of hydrogenase (the enzyme that releases molecular H₂ gas) activity was well recognized by the 1970s, and represented a major practical challenge limiting the ability of algae to generate hydrogen as a renewable source of energy. One of the very first attempts to address this problem was made by Robert (Bob) K. Togasaki and his co-workers (see McBride et al. 1977), who generated hydrogenase mutants that were less sensitive to O₂, as was shown by using a positive selective pressure, based on reversible hydrogenase, i.e., the H₂-uptake activity. Since this approach produced mutants with high levels of the oxyhydrogen reaction, we decided in the 1990s to test an alternative approach (applying selective pressure involving a H₂-production mechanism), which we thought, from an application perspective, to be more successful. Anthony (Tony) G. San Pietro (1922–2008), who was a regular visitor to our laboratory at the time, suggested that we discuss this problem with his friend Bob Togasaki (both were professors at Indiana University in Bloomington, Indiana). It turned out that Bob was on his way to visit Arthur Grossman's laboratory at the Carnegie Institution of Washington (at Stanford) at the end of October 1994, as a part of his sabbatical year. When we invited him to stop by at National Renewable Energy Laboratory (NREL) in Golden, CO, and give a seminar, he gladly accepted and visited us for a couple of days. Among numerous discussions with many at NREL, we included the problem of a new type of selective pressure. Bob recommended that we examine possible competition at the level of ferredoxin in Photosystem I (PSI) between the added metronidazole (see Asada 1984) and H₂-production activity. Together with Maria Ghirardi, my postdoc at the time, we discussed how metronidazole might be employed to provide the selective pressure. H₂-production activity of any surviving mutants in the presence of O₂ could be used to determine success of the selective pressure. During subsequent months, while in telephone consultation with Bob, we worked out the details of a successful experimental selective approach and obtained a number of *Chlamydomonas*

reinhardtii mutants for testing. Two of the mutants that we isolated were much more tolerant to O₂ compared to the wild-type with no change in the initial H₂-production velocity of the reaction. Most of the others, though, while less sensitive to O₂, were impaired in electron transport activity. For details about the mechanism of the selective pressure, how it works in practice, and the assay method for validating the results, see our joint publication (with Togasaki; see Ghirardi et al. 1997). As of August 2021, this article has been cited almost 300 times. Subsequent, unpublished observations have demonstrated that the mutants in the absence of constant selective pressure revert quickly to wild-type properties. We also suspect that the mutants reported may not have been hydrogenase mutants *per se*, but possibly ancillary mutants involving enzymes associated with the deactivation of active O₂ species. In our view, Bob was the perfect collaborator with a great handle on the photosynthesis literature. He was also a source of sage advice, and had a kind, humble way of interacting with everyone in the lab. He was a great mentor to all of us during our work together. The development of 'BioNeb' by Bob Togasaki, together with Stefan Surzyki and M. Kitayama (see above for details) for fragmenting algal cells and DNA is well known to all of us. As the result of Bob's visit, we in fact bought one for our lab, and it has gotten a lot of use over the years, leading to several later publications. We all miss Bob Togasaki.

Jon Suzuki (Research Molecular Biologist, United States Department of Agriculture-Agricultural Research Service, Daniel K. Inouye U.S. Pacific Basin Agricultural Research Center; e-mail:jon.suzuki@usda.gov)

I first met Bob Togasaki when I visited the Indiana University campus as a prospective graduate student. I learned of Bob's caring nature from that very beginning. He was thereafter, starting in 1988, always a part of my graduate school life. Although I did not end up in his lab, he graciously agreed to be on my doctoral thesis committee. I learned important fundamentals of photosynthesis in classes with him. I was also one of a line of graduate students who led undergraduates through experiments in Bob's famous Cell Biology laboratory course; he was always interested in the use and the development of innovative devices to advance research in biology. Through him and his doctoral student at that time, Masahiko Kitayama, my adviser Dr. Carl Bauer and I were able to use biolistics to knock out a chloroplast gene important for chlorophyll biosynthesis in the dark in the cells of the green alga *Chlamydomonas*, Bob's favorite organism (see e.g., Suzuki 1992, and Kitayama et al. 1995a, b). He was frequently seen whisking down the halls of the biology building, folders in hand; at such times, try as I



Fig. 7 Top Left: Robert Togasaki (on the extreme right) with Yasuhiro Kashino (University of Hyogo, Japan), in the middle and his wife Natsuko Inoue-Kashino, undated. Source: Teruo Ogawa. Top Right: Robert Togasaki is celebrating, by sharing Champagne with Lab members (left to right: Ken Spencer, Arthur Grossman, Bob,

a student from another lab, and Peggy Hudock, (Bob's technician), when one of their papers was accepted in a top journal, undated. Source: Charlene Forest. Bottom: Left to right: G. Govindjee (one of the authors), Robert Togasaki, and Krishna Niyogi (of UC Berkeley) at a 2014 conference in Stanford, California. Source: Rajni Govindjee

might, it was hard to keep up with him. Though he was an eminent researcher and professor, he was always very warm, humble, and approachable. Bob was a consummate mentor and a true and loyal friend. He expended exhaustive energy to champion his students such as myself, as well as colleagues in need. Though Bob was slight of build and a most reserved person, he once bear-hugged me completely off the ground upon hearing that I had finally passed my qualifying exams, which allowed me to continue the path towards my Ph.D. I will always remember his humanity and he continues to inspire and uplift me in my research and life to this very day.

Epilogue

Bob Togasaki was not only a top researcher, an inventor, and an extraordinary teacher, who cared for all (including many adopted cats!), but he also enjoyed the arts. In addition, he enjoyed being with scientists around his university as well

as the World. Figure 7 shows him with many others showing his international comradery.

We are told that often Bob was deeply involved in listening and enjoying Rakugo Japanese Comedy and would discuss in-depth, its nuances with friends and family. Further, his unique association with Crown Prince Akihito of Japan reflects on his quality as an extraordinarily friendly human being among us. He leaves behind his sister, Betty Emiko Shibata, three nieces Taeko Togasaki, Sumiko Togasaki, and Emily Ayako Sato, and a nephew, Mark Makoto Shibata. He is preceded in death by his parents, wife Fumiko, and a brother Gordon Togasaki. Bob is greatly missed by all in his family, his friends, his many past research collaborators, and students (see [Reminiscences](#)) including all the authors of this Tribute.

Acknowledgements We are thankful to all those who wrote "[Reminiscences](#)" of Bob Togasaki and provided an in-depth thoughtful picture of this wonderful human being who had touched hearts of many. We give special thanks to Charlene Forest who gave us several photographs, used in this Tribute. We also thank the Department of Biology of

Indiana University at Bloomington, for providing us access to information on Bob Togasaki.

Author contributions GG initiated the writing of this Tribute; SC wrote the first draft and collected the Reminiscences; GG and CB contributed to the writing and the editing of the final text.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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