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NEWS REPORT

William L. Ogren was honored with a Lifetime Achievement Award by the Rebeiz Foundation for Basic Research

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Abstract This *News Report* is a brief description of the 2010 Lifetime Achievement Award received by William (Bill) L. Ogren from the Rebeiz Foundation for Basic Research, at Champaign, Illinois, on Sep 10, 2011. It focuses mainly on the presentations by two of us (ARP and Gov), Christoph Benning (on behalf of Chris Somerville), David Krogmann and Jack Widholm, at this ceremony. It is enriched by the testimonial received from George Bowes at the time of the preparation of this report.

Keywords *Arabidopsis* · Photorespiration · Rubisco · George Bowes · William Laing · Chris Somerville

William L. Ogren, former research leader of the Photosynthesis Research Unit, Agricultural Research Service, US Department of Agriculture (USDA) and former Professor of Agronomy (now Department of Crop Sciences) and of Plant Biology at the University of Illinois at Urbana-Champaign (UIUC), was honored during a ceremony on Sep 10, 2011, at the Rebeiz Foundation[1] for Basic Research headquarters in Champaign, Illinois. Over 60 guests (Fig. 1), including Christoph Benning, Govindjee, Archie Portis, Constantin (Tino) A. Rebeiz, and Carole Rebeiz, representing all the members of the Board of Directors of the Foundation, attended the ceremony. The ceremony included a buffet style dinner, and testimonials by Govindjee (UIUC), Archie Portis (formerly with the Photosynthesis Research Unit, USDA), Jack Widholm (a former colleague at UIUC), Christoph Benning, speaking for Chris Somerville (a former post-doctoral associate) who could not attend and David Krogmann (Bill's PhD advisor). Tino Rebeiz (President of the Foundation) presented a recognition plaque, and a monetary award, to Bill Ogren (Fig. 2, left). Figure 2 (right) shows Ogren with others who gave presentations.

The Board of Directors of the Rebeiz Foundation for Basic Research had selected Dr. William L. Ogren for the

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[1] Rebeiz Foundation: The Rebeiz Foundation for Basic Research (a tax-exempt institution, located in Champaign, Illinois) is dedicated to the promotion of fundamental research at the national and international levels. Among other things, the Foundation (www.vlpbp.org) sponsors national and international research on chloroplast chemistry, biochemistry and molecular biology. In order to promote the best research on chloroplasts it delivers an annual prize for the best paper in the field. The Foundation is run by a group of scientists that includes a President of the Board [C. A. (Tino) Rebeiz], and ten Board Directors that represent eight chloroplast research areas of interest. Current members are: Thomas Bach, University of Strasbourg, France; Don Bryant, Pennsylvania State University, USA; Christoph Benning, Michigan State University, USA; Henry Daniell, Central Florida University, USA; Govindjee, University of Illinois, USA; William Lucas, University of California at Davis; Harald Paulsen, Johannes Gutenberg University Mainz, Germany; Archie Portis, University of Illinois at Urbana-Champaign; Thomas Sharkey, Michigan State University, USA; Baishnab C. Tripathy, Jawaharlal Nehru University, India; and Carole Rebeiz, Rebeiz foundation for Basic Research, Secretary.

Fig. 1 Photograph of attendees at the award ceremony. William Ogren is sitting in the 2nd row, 3rd from right; next to him is David Krogmann (his PhD advisor; 2nd from right); Carolyn Ogren, Bill's wife is 4th from right. Carole and Tino Rebeiz are 3rd and 4th from right in the first row. Photo by Laurent Gasquet

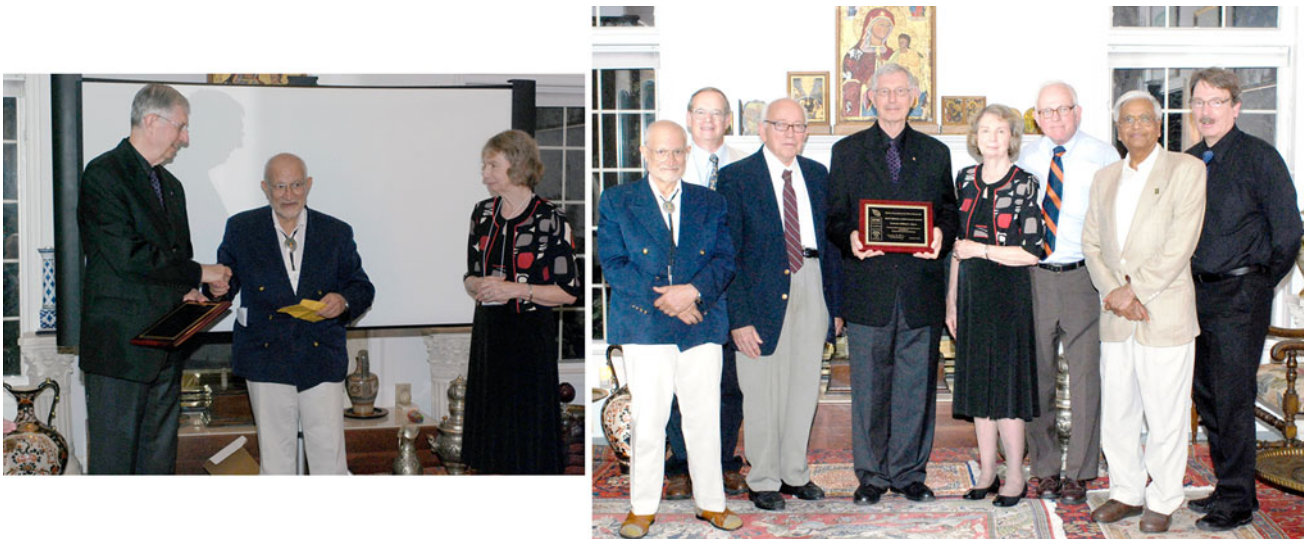

Fig. 2 *Left* Photograph of William (Bill) Ogren (*left*) receiving the Award from Constantin (Tino) A. Rebeiz (Foundation president; *middle*); Carolyn Ogren (wife of Ogren; *right*). *Right* Photograph (*left to right*) Tino Rebeiz, Archie R. Portis (testimonial), David W. Krogmann (testimonial and Ogren's Ph.D. advisor), William L Ogren, Carolyn Ogren, Jack M. Widhom (testimonial), Govindjee (testimonial), and Christoph Benning (testimonial from C.R. Somerville). Photos by Laurent Gasquet

2010 Lifetime Achievement Award[2] in recognition of his distinguished career and leadership in photosynthesis research. Dr. Ogren's plaque reads:

> For his scientific achievements and original research in the fields of Photosynthesis and Photorespiration.

Further details of the ceremony, testimonials, and pictures can be viewed at the foundation website (http://www.vlpbp.org/#RFFBR%20LifeTime%20Achievement%20Awards). Ogren's leadership abilities have been widely recognized by his peers and he has served in many capacities at national and international levels. These are too numerous to mention here. Also he has received many national and international awards previous to his recognition by the Rebeiz Foundation. We will only mention two upfront—those we think are the most significant in that they also indicate the breakthrough nature of his

[2] Previous Lifetime Achievement Awardees of the Rebeiz Foundation for Basic Biological Research are: Govindjee (2006; see C.A. Rebeiz et al. (2007) Photosnthesis Research, volume 94, pp 147–151); Paul Castelfranco (2007); Andrew A. Benson (2008; see Govindjee (2010) Photosynthesis Research, volume 105, pp 201–208); and Diter von Wettstein (2009). Web pages are given within parentheses: for Govindjee (http://vlpbp.org/govindjeeltachmtaward032607a.html); for Paul Castelfranco (http://vlpbp.org/ltaawardcastelfrancoceremonyfinal%20092408b.htm); for Andy Benson (http://vlpbp.org/ltaawardbensonceremonyfinal%20112909a.htm) and for Diter Von Wettstein (http://vlpbp.org/ltaawardvonwettsteinceremony093010a.html).

contributions to science and agriculture. First, in 1986 he was elected to the National Academy of Sciences (USA) and second in 1990 he received the Alexander von Humboldt Award for having made the most significant contribution to American agriculture during the previous 5 years (for further details, see Govindjee's testimonial).

A summary of the presentations, as modified for this *Report*, at the ceremony follows.

David Krogmann

Ogren conducted his PhD research under the supervision of David Krogmann. Ogren had enrolled for graduate studies in the Chemistry Department as an evening student at the Wayne State University shortly before the beginning of classes in the fall of 1961. At that time, he was employed as a chemist at the Parker Rust Proof Company working on inorganic conversion coatings, chemical products that ameliorated corrosion and provided superior paint bases. His research interests at the time were inorganic and analytical chemistry but it turned out that the only night course offered in Chemistry that year was Krogmann's biochemistry class, and so he enrolled in it. About two-thirds of the way through the year, Krogmann offered a Teaching Assistantship. After considerable thought, Ogren resigned from his position at Parker and joined Krogmann's laboratory in the summer of 1962.

We present Krogmann's testimonial. An excerpt from his talk is:

> I arrived at the Wayne State University in Detroit in 1961. I was teaching an evening class in biochemistry. A few weeks of classes and an exam revealed that Bill Ogren was the best of the thirty students. Immediately, I asked Bill to consider post-graduate studies. A week later, Bill decided to enter the MS/PhD program. He became a fine bench worker and a man of powerful intellect. He graduated in 1965 and his PhD thesis was perfectly written; it explained his work on the roles of pyridine nucleotides in photosynthesis and respiration. After graduation, he began his career at the USDA. Bill, we want to congratulate you on this special evening and for this well-deserved award.

Govindjee

Govindjee (one of the authors), a long-time associate of Bill Ogren at the UIUC, gave a short presentation recalling their good days as teachers in a joint course on "Photosynthesis" for graduate students, where they had great fun together (Fig. 3); several of their students became professors or administrators elsewhere. Many of these students remember Bill through his thorough lectures; they respected him for what he gave them.

Govindjee began his talk by saying "We honor you Bill today in Champaign-Urbana, where your noted scientific achievements for the award were made", and then he congratulated him on the 2010 Lifetime Achievement Award of the Rebeiz Foundation. This was followed by a question "Who is this man?" A brief description of his academic career and some key honors of Bill Ogren were mentioned. He said William Lewis Ogren is a world-class plant physiologist, and a biochemist of the highest order, but most importantly Bill is a *great human being*. (See the pdf file at: http://www.life.illinois.edu/govindjee (see under "Announcements"). Then he mentioned his education and awards: BS in 1961 from the University of Wisconsin; PhD in 1965 from the Wayne State University (see David Krogmann's testimonial); Member of the National

Fig. 3 A photograph of the 1969 class on "Photosynthesis" (Govindjee and William Ogren, instructors). *1st row* (*Left to right*): Glenn Bedell; unidentified; Christine Grant (Newell); Govindjee; and William Hough. *2nd row* (*Left to right*): Alan Stemler; Ray Chollet; Melvin Markowitz; and Tom Guilfoyle. *3rd row* (*Left to right*): Thomas Threewitt; Gary Wells; Harold Coble; Prasanna Mohanty; George Bowes; and William Ogren (also see Ogren 2003)

Fig. 4 William Ogren (*left*) receiving an honorary Doctor of Science (D.Sc.) degree from Chancellor John D. Wiley, University of Wisconsin-Madison (2006) (Photo: courtesy of University of Wisconsin-Madison; received via Bill Ogren)

Academy of Sciences USA (Plants, Soil and Microbial Sciences) in 1986; Charles F. Kettering Award for Excellence in Photosynthesis Research, American Society of Plant Biology (ASPB), 1986; recipient of the Alexander von Humboldt Foundation Award, 1990; President of the ASPB, 1990–1991; and Agriculture Research Service (ARS) Science Hall of Fame inductee, 1997. Figure 4 shows William Ogren (left) receiving an honorary Doctor of Science (D.Sc.) degree from Chancellor John D. Wiley, University of Wisconsin-Madison (2006). It was indeed a high honor.

Govindjee specifically mentioned the research perspective Bill wrote for him (Ogren 2003; see testimonial of Archie Portis). He mentioned that here Bill mostly recognized others, and that *his humility gives Bill away anywhere!*

Govindjee did, hesitatingly, mention two scientific interactions with Ogren's research group: (1) was a mini-review, with Doug Jordan, in 1980, on the possible role of bicarbonate in the "light reactions of photosynthesis" (Jordan and Govindjee 1980), and (2) was a small piece of research that he did with Bill: influence of CO_2 on the growth and chlorophyll a fluorescence of the green alga *Chlamydomonas*: it was not in the main stream of Bill's research, but it was great fun for all those who were involved in it (Spalding et al. 1984).

Chris Somerville

Chris Somerville made fundamental discoveries while working with Ogren (see section by Archie Portis). Since, Chris was unable to come to the ceremony, his testimonial was read by Christoph Benning. Somerville wrote:

> I am delighted that Bill (Ogren) is being honored with this award—and particularly that these remarks are to be read by my former student Christoph Benning, a scientific grandson of Ogren. I arrived in Bill Ogren's lab in 1978 with no knowledge of photosynthesis or plant biology. By the time I left in 1981 we had created some new thrusts in both topics that fueled a lot of subsequent discovery. That was only possible because Bill was a brilliant and very supportive mentor who always pointed me in productive directions and provided both a theoretical basis and a lot of practical advice for everything we pursued. I not only learned plant physiology from Bill, but also how to support and motivate younger scientists (such as Christoph Benning). Those of us who studied with Bill were unusually lucky to have had not only the advice of one of the major figures in photosynthesis, but also someone who was wise and generous and thoughtful—a model scientist in my experience.

Archie R. Portis

Archie Portis (one of the authors) summarized the research and leadership accomplishments of William (Bill) Ogren, as follows.

With George Bowes: 40 ago (1971), Ogren's research group published two revolutionary papers directly linking photosynthesis and photorespiration via one enzyme. In the first article (Ogren and Bowes 1971), through a perceptive comparison of photosynthesis and photorespiration in leaves with the oxygen inhibition of carboxylation by the isolated enzyme, Ogren and a postdoctoral associate, George Bowes, reasoned that photorespiration is initiated by the same enzyme that initiates photosynthesis. They speculated that the enzyme catalyzed an alternative reaction, which uses O_2 rather than CO_2. In the second article (Bowes et al. 1971), they proceeded to demonstrate that indeed O_2 was a substrate and this reaction produced phosphoglycolate, an immediate precursor to the long-sought source of glycolate, the substrate of photorespiration (see the write-up by George Bowes). The enzyme is now known as ribulose bisphosphate carboxylase/oxygenase (Rubisco) as a result of this discovery (see also Wildman 2002).

With William (Bill) Laing: Ogren and Laing then verified that this enzyme controlled both photosynthesis and photorespiration by quantitatively relating the enzyme's carboxylation and oxygenation kinetic constants to the

photosynthetic response of leaves to O_2, CO_2, and temperature (Laing et al. 1974).

Ogren's 2003 perspective: The whole field of photorespiration and its relationship to photosynthesis was highly controversial and this series of papers from Ogren's lab was not widely accepted and generated even more controversy for several years. Ogren's retrospective, published at the invitation of one of us (Govindjee), in *Photosynthesis Research* (Ogren 2003), provides details about the resistance he faced. The research formed a unifying theory of photorespiration which finally explained: (a) the coincident oxygen inhibition of photosynthesis [the "*Warburg Effect*", first reported in 1920 (Warburg 1920)]; (b) the oxygen stimulation of photorespiratory glycolate synthesis and CO_2 evolution; and (c) reversal of these effects by CO_2 (see a review by Ogren 1984). We emphasize here that the equations developed by Laing et al. (1974) provided the foundation for all kinetic models of photosynthesis, including those currently used to predict the response of plant performance to the rise in global CO_2 concentration and change in temperature, topics that remain of major concern. (Richard Hageman, who died in 2002, was a plant physiologist and a professor of agronomy at the UIUC whose collaboration in this project was very helpful.)

With Chris Somerville: Having found that the same enzyme was the starting point for both processes, Ogren quickly realized that one approach to decrease the detrimental photorespiratory process was to directly modify the enzyme and not to block the photorespiratory process, which was being promoted by others. This attracted the attention of a young researcher, Chris Somerville, who came to the lab. Chris thought that a relatively unknown plant, *Arabidopsis* would be a useful model system for a genetic approach to the controversy. Their collaboration resulted in the creation and detailed characterization of the first directed nuclear gene mutants in a higher plant (*Arabidopsis*), in this case with defects in photosynthetic carbon metabolism (e.g., Somerville and Ogren 1979; also see Somerville 1982; and Somerville 2001). We note that other nuclear gene mutants in higher plants were known. What Chris did was to make the first plant nuclear gene mutant with lesions in a specific physiological process. These were not just the first plants with predetermined lesions in photosynthesis, but the first with predetermined lesions of any kind. That is why the experiments are so important. With these mutants they were able to genetically dissect the pathway of photorespiration and provide definitive answers to several remaining and controversial aspects of photorespiratory carbon metabolism. These pioneering studies were instrumental in establishing the usefulness of *Arabidopsis* as a model genetic system for higher plants and launched the careers of many scientists. One of the mutants isolated by Chris Somerville was characterized as being defective in the light-induced increase in the activity of Rubisco (Somerville et al. 1982). Previously, this was generally thought to occur spontaneously in response to the concentrations of CO_2 and magnesium and the pH around the enzyme. But this mutant clearly indicated that another factor was involved in the "light activation" of Rubisco.

With Douglas Jordan: Meanwhile, Ogren and a graduate student, Douglas (Doug) Jordan, also initiated studies directed at understanding the biochemical factors that determine the specificity of the enzyme for CO_2 versus oxygen. They developed a convenient method to accurately assay specificity and discovered that an order of magnitude variation in the enzyme's specificity occurs naturally in diverse photosynthetic species (Jordan and Ogren 1981). They reasoned that this variation was an evolutionary response to the natural environment and geological changes in the composition of the atmosphere. In view of the global climate change, challenges remain high, but this research provides the basis for the continuing optimism in many labs throughout the world since Rubisco can be modified to improve the photosynthetic efficiency of crop species through appropriate changes in enzyme structure.

With Mike Salvucci and Archie Portis: The *Arabidopsis* mutant that Chris Sommerville had isolated languished in the lab for a few years. However, Ogren encouraged a new postdoc, Mike Salvucci and one of us (ARP)—still a relatively young hire, looking for an important research focus—in a renewed attack to identify what was exactly wrong with this mutant. In 1985 with some good fortune, Salvucci et al. (1985) were able to establish genetically, physiologically, and biochemically that the activity of Rubisco is regulated by another protein, which was named Rubisco activase (Salvucci et al. 1985). The isolation and characterization of the heretofore unsuspected Rubisco activase protein resolved several long-standing dilemmas regarding the regulation of Rubisco activity (see Portis 2003).

Figure 5 shows a 1985 photograph of William Ogren and Michael Salvucci examining the protein gels which first demonstrated the physical existence of Rubisco activase. Two related Rubisco activase proteins were identified by comparing extracts of *Arabidopsis* wild-type and a Rubisco activase-deficient mutant (see Portis and Salvucci 2002).

With Jeff Werneke: Ogren and graduate student Werneke followed up these studies by taking advantage of recently developed molecular biology tools to isolate the gene and thereby discovering that the expression of the protein involves an alternative pre-mRNA splicing process (Werneke et al. 1989). This was the first characterization of such a process in a plant. Subsequently, Mike Salvucci and colleagues were able to show that an unusual heat sensitivity of Rubisco activase, that had been found earlier, was

Fig. 5 A 1985 photograph of William Ogren (*left*) and Michael Salvucci examining the protein gels which first demonstrated the physical existence of Rubisco activase (see Portis and Salvucci 2002)

a key factor in the reduced photosynthesis of many important crop species at high temperatures (Crafts-Brandner and Salvucci 2000). Many groups around the world continue to study Rubisco activase with the ultimate goal of determining whether alterations will be able to improve the photosynthetic efficiency of plants.

Ogren's remarkable mentorship: The Lifetime Achievement Award also recognizes that in addition to his own extraordinary research accomplishments, Ogren has provided outstanding leadership as a mentor and leaves a scientific legacy that includes a remarkable progression of students and postdoctoral associates. Less well known outside the UIUC campus is the fact that he was instrumental in several highly successful USDA and University of Illinois at Urbana-Champaign faculty hires. Several of these students, postdocs and faculty have become world leaders in their own right. One of the more compelling, but lesser-known examples of his excellence in recognizing and promoting young talent is that he successfully nominated one of his graduate students, Jeff Werneke, for a quadrennial award in 1989 from the Council of Graduate Schools for the Distinguished Dissertation in Biological Sciences.

Jack Widholm

We end this News Report of the Ceremony where Ogren was honored with a testimonial by Jack Widholm; Jack continues to work at the UIUC, and has known Bill Ogren for more than 40 years. The Widholm and Ogren families are close friends. Jack wrote:

> It is a great honor for me to be a part of the Ogren Lifetime Achievement Award Ceremony. We have done work together and been friends since 1968. I am not a photosynthesis person but in 1967 when I was working at the International Minerals and Chemical Corporation in Libertyville, Illinois I had an idea about how to screen for plants that lacked photorespiration. The idea was to grow C3 plants under low CO_2 conditions below the CO_2 compensation concentration where they would lose CO_2 and die. I wrote a letter to the USDA to get funding, I got none, but the letter made it to Bill in USDA *and he responded that it might be a good* idea. Interestingly in May 1968, I joined the Agronomy Department at the University of Illinois at Urbana-Champaign (UIUC), and, thus, Bill and I worked together on the idea (Widholm and Ogren 1969). We showed that indeed C3 but not C4 plants would die under low CO_2; we then screened the oat collection and about 350,000 mutagenized soybean plants with no survivors! (For a historical perspective on C-3 pathway, see Benson 2005; and Bassham 2005; and for C-4 pathway, see Hatch 2005.) Clearly, if we had succeeded in eliminating photorespiration, the yields of many crops would have increased greatly, but we did not, and later work by Bill Ogren and Chris Somerville with *Arabidopsis* showed that the photorespiratory pathway cannot be blocked and still have viable plants. Thus attempts to alter *Rubisco* to not react with oxygen have not yet been successful. This work with *Arabidopsis* mutants opened up a most important research area using *Arabidopsis* as a plant model species (see the above testimonial by Portis).
>
> I always admired Bill since he was such a thinker who persevered and solved complex problems like the mechanism of photorespiration that clearly is a landmark discovery. His approach was the key to being a great scientist and the awards he has won, including this one, have been justly deserved. Along the way he also helped nurture a group of very astute researchers.

George Bowes

As noted in the write-up by Archie Portis (see Ogren and Bowes 1971; Bowes et al. 1971), the first observation that gave the idea that the same enzyme (known earlier as "carboxydismutase" in Melvin Calvin's lab) was responsible for reaction with CO_2 and O_2 evolved in the work of Bill Ogren with George Bowes, who was a postdoctoral associate at the University of Illinois at Urbana, Illinois. Although George was unable to attend the ceremony, he was invited by the two of us to present his story.

George sent the following text to us. It reads:

> I was Bill's first postdoc. I came to the US in 1968 at Richard (Dick) Hageman's invitation, but when I

Fig. 6 Ambiance at the Rebeiz foundation on the day of the award to Bill Ogren. *Top left* Some of the audience listening to the presentations on Ogren. *Top right* (*left to right*): Archie Portis; Christoph Benning; William Ogren; and David Krogmann. *Bottom left* Guests at the bar. *Bottom right* William Ogren (*3rd from left*); and Jack Widholm (*7th from left*). Photos are by Laurent Gasquet, except the one on *top right* that is by Govindjee

arrived he gave me a choice—to work on nitrogen metabolism or work with a "young USDA scientist" (Bill Ogren) on photosynthesis. Knowing little about either topic I asked for a week to decide and Bill gave me some papers, including one by Olle Björkman that contained a graph showing carboxydismutase (Rubisco) activity was directly related to photosynthesis rate. It convinced us both that this was an important enzyme, and could be a productivity "marker" in soybean varieties—a topic we pursued prior to purifying the enzyme and investigating its kinetic characteristics.

Working with Bill was an enjoyable and productive learning experience. Coming from a largely self-directed PhD program, I appreciated being a collaborator, not someone to "direct", and this laid-back leadership style of his has produced some remarkable scientists and discoveries. Bill was easy to talk with, very prescient and direct and could take a half-baked idea and hone it into something useful. I recall Friday afternoons when we would chat about everything from English customs (Bill was an anglophile) to politics and sports. This Englishman/American learned a lot about American life from Bill. Inevitably, the talk turned to the recent discovery of C-4 photosynthesis and the mechanism of the Warburg effect (Warburg 1920). These casual conversations were some of the most productive times of sharing ideas to test experimentally. Later Bill Laing and then Ray Chollet joined the lively prolonged coffee hours.

I am thankful that neither Bill nor Dick gave up after the first year of research when I had no publishable results to report, and was quite discouraged. But due to Bill's patience and support, things turned around on Dec 13, 1969 when the data came off Bill Rinnie's liquid scintillation counter showing that RuBP (then called RuDP) carboxylase (Rubisco) activity was reduced when the reaction was run in 21 or 100% O_2 relative to N_2. I left to spend Christmas with my family in London and Bill was away so he did not know that we had succeeded until I returned in January. We repeated the experiment with newly

purified enzyme on Jan 23, 1970 and came up with a near perfect Michaelis–Menten competitive effect.

Finding phospho (P)-glycolate took much longer than we anticipated—over a year—due to difficulties in designing an enzymatic/spectroscope method to measure P-glycolate that was free of interfering compounds. Bill was eager to persevere. Thanks to his enthusiasm—on May 20, 1971, after many failed attempts, we were able to measure a P-glycolate production rate by RuBP carboxylase. It took even longer for the concept to be fully accepted that this enzyme was the source of the "Warburg effect" and photorespiration. Thanks largely to later exceptional discoveries in Bill's lab; it is now an introductory textbook dogma.

Bill richly deserves this recognition: the Lifetime Achievement Award given to him in 2011. He is an outstanding scientist, and it was an honor to work with him in those early years. His mentoring and support has launched others on very successful careers, and I look back to my time with him in Illinois as the foundation that led to a very rewarding scientific career for me—for which I am very grateful.

The above testimonial by George Bowes sums it all up. We end this tribute with a photo plate that shows some of the guests and the great ambiance that was provided by Carole and Tino Rebeiz on the day Bill Ogren was recognized right in his own hometown of Champaign, Illinois (see Fig. 6).

Acknowledgments We thank Carole and Tino Rebeiz for all the hard work they did in organizing such a wonderful event. We thank Tino Rebeiz for providing photographs from the foundation website (taken by Laurent Gasquet); we also thank him for suggestions for the improvement of this manuscript. We are thankful to Alex Goloff, a former student of Plant Biology at the UIUC, for reading this Tribute to Bill Ogren. We appreciate the comment he made when he wrote to us: "The photosynthesis 'cadre' is most fortunate to have someone like you to spearhead the praise, merits, honors, and formal awards for fellow colleagues".

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