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Obituary

Ed Tolbert and his love for science: A journey from sheep ranch continues. . .

Nathan Edward (Ed) Tolbert (1919–1998)

On December 13, 1998, Nathan Edward (Ed) Tolbert died at the age of 79 in East Lansing, Michigan, USA. Ed was in his office working most of the day on Friday, December 11, 1998 prior to his planned departure to Boca Raton, Florida, on Saturday. He used to live in Boca Raton with his wife Eleanor Tolbert during the chilling winters of Michigan where his activities included a daily walk on the beach, day dreaming science in the balcony of his condominium, reading current and historical scientific literature, critical thinking, and writing manuscripts and his thoughts. Since 1991, he had been developing a new concept of Oxygen Compensation Point in plants and algae and its role in the regulation of atmospheric levels of CO_2 and O_2. Ed kept his research collaborators Erwin Beck (Germany), Yoshi Shiraiwa (Japan) and Arun Goyal (USA) busy and excited with his long weekly letters describing new thoughts and encouraging them to design and perform experiments to address various aspects of the oxygen compensation point.

Ed Tolbert was born on May 19, 1919, on a farm outside Twin Falls, Idaho, the oldest of four children of Edward and Helen Mills Tolbert. As a young boy, Ed worked at many jobs on his father's farms, including, but not limited to, planting, cultivating, irrigating, weeding, stacking hay, harvesting, lambing and more, as well as the usual daily milking chores. His father was both a very capable farmer and good businessman who went to Alaska during the gold rush in 1890, so the family prospered and there was adequate money to send all the children to college, even in the depression years. Since he and his brothers and sisters were raised during the depression years, they were all taught to be very careful in their use of money, a characteristic of Ed that all his friends and colleagues were well aware of. While his moral development was guided by both of his parents, much of his academic and professional development during this period was guided by his mother, herself a remarkable woman, who graduated from Grinnell College in 1911 and then obtained a Master's degree in English at the University of Chicago. She was a liberal person who wanted her children to have the best education possible.

Ed went to a small rural country grade school, Curry School District #8, in Twin Falls County, Idaho. The school building still stands, now as a historic museum on US-30, a few miles west of Twin Falls. It consisted of only three rooms with three teachers, with a class size of about 10 students per grade, and room for some 30 students. The school was served by a horse-drawn covered wagon as the 'school bus'. The educational program taught only three basics: reading/writing, arithmetic and history, and baseball as the primary action sport. The courses were well taught by three young but competent teachers. His mother played a key role in Ed's overall primary education by supplementing the basics with more diverse knowledge each night around a kerosene lamp that Ed used to call 'Nightly Drill'.

Ed's Twin Falls High School class graduated about 200 students. He stood out as Class Representative, and he was active in extracurricular activities including Thespians, even though he had only limited after-hours transportation to and from school and many chores at home. His first two college years were spent at Idaho State University in Pocatello, Idaho, where he majored in Chemistry. He did well both in academics and in the broader social world. After two years at college, his father suggested that if he returned home, he would buy him a sheep ranch in Sun Valley. Ed's mother wanted him to go to Grinnell College or one of the named eastern schools, but because of the growing reputation of the University of California at Berkeley in the sciences, she urged Ed to apply there. At that time, the Bay area was alive with a great World's Fair on Treasure Island. Ed lived at a liberal men co-operative, Barrington Hall, which was a block long apartment house converted for student use. There, as Ed eventually found out, you were deemed very conservative if you were a democrat, just possible as a socialist, and you were on the forefront if you advocated communist philosophy or better a member of the party. Ed worked hard at his studies and then returned each summer to the Idaho farms to help his Father.

When Ed graduated (BS in Chemistry) from the University of California (UC) at Berkeley in 1941, he took an organic research chemist's job ($150 per month) in the Department of Viticulture and Enology at UC Davis, working with America's foremost Wine Connoisseur, Maynard Amerine. At Davis, Ed shared a house with Maynard Amerine and A. Dinsmore Webb where he learned the art of wine tasting. His first publications were in the *Journal of Food Research*, on pH (Tolbert et al. 1943) and tannins (Guymon et al. 1943). In the Chemistry Department at UC-Berkeley, Ed's senior thesis was on light-activation of silver halides. Ed enlisted in the US Army Air Force in 1943. On the basis of his senior research, he applied to the Air Force for officer training as a photographic expert. Ed was trained as a Photo Intelligence Officer in Florida and Yale University, and his first assignments were in Connecticut and Florida. After becoming an officer, he was sent to the Pacific area as the renewed attack to recover the Philippines and other islands got underway. He suffered a rifle bullet wound in one leg, but was very fortunate that a coin in his front pocket deflected the slug, so that what would have been a devastating femur break was only a muscle wound. After recovery in Australia, he went on to become part of the Occupation Force for Japan. The journey that started at the sheep ranch in Idaho continued after the World War II to Midwest town of Madison in Wisconsin.

At UC-Berkeley, Ed was challenged by an intensive course in Biochemistry. At that time, the first radioactive, $^{11}CO_2$ photosynthetic experiments were done by Sam Ruben (until he was killed by phosgene gas), while Ed was working in a nearby laboratory. Ed came out of the World War II with a very clear purpose – to get graduate education in biochemistry. He applied for and was readily accepted at what was then considered the Number 1 School in Biochemistry, the University of Wisconsin, Madison. Ed was fascinated by the opportunity to canoe in Madison during the evening breaks from the research laboratory. At Wisconsin, his work with Prof. Bob Burris, who was to become one of his long-term mentors, stimulated his interest in photosynthesis. After completing his PhD in 1950, Ed returned to UC-Berkeley to spend a year as a postdoctoral researcher in Melvin Calvin's laboratory of photosynthesis in 1950, working on aspects of carbon metabolism (identifying and isolating sedoheptulose 7-P, xylulose 5-P, P-glycolate and glycolate), a problem that eventually developed into a major lead on his work on sedoheptulose, Rubisco and peroxisomal metabolism in plants and animals (Clagett et al. 1949; Tolbert et al. 1949; Tolbert and Burris 1950; Calvin et al. 1951a,b; Benson et al. 1952; Tolbert and Zill 1954a,b, 1956).

Following one year as a post- doctoral fellow, Ed took an administrative job at the Atomic Energy Commission (AEC) headquarters in Washington, DC. For two interesting years, during which he moonlighted with S. Hendricks at the United States Department of Agriculture (USDA) in Beltsville and R. Withrow at the Smithsonian Institution to study activation of glycolate oxidase in etiolated leaves, while administering granting of funds for AEC (Tolbert and Pearson 1952). Ed used to say that after two years he became 'wiser' because he realized that he was too young to get out of research so soon, and giving out dollars was not going to get him much further in science. Therefore, he elected to go back to research at the Oak Ridge National Laboratory in Tennessee. When Ed left Washington DC, he made a firm commitment that he would never take another administrative job in his life. At Oak Ridge, he worked in the Biology Division of Alexander Hollander, a crusty, but benevolent, boss who gave him the encouragement, facilities and freedom he needed to develop his ideas in plant biochemistry. He did well at Oak Ridge, starting a family and publishing a number of significant papers on glycolate metabolism.

In 1958, Ed was recruited by Guarth Hansen to Michigan State University (MSU) as Professor of Agricultural Chemistry. A few years later, Ed was one of the visionaries to form a new Biochemistry Department with responsibilities for programs in four colleges of the University. Ed made major contributions toward the development of a strong research and graduate training program in the Department. In the early 1960s, federal and matching funds were obtained and a new Biochemistry Building was designed with the greatest input into laboratory design from Ed. As a major sacrifice to his research program, Ed spent two years at the new building site working out the details and solving construction problems with the contractors and architects. This building stands as a prototype as to how a biochemistry building should be designed and built. Its ability to serve admirably the needs of laboratory work 35 years later attests to Ed's contribution as a team player, quite apart from his independent and highly successful research program. Ed was also instrumental in the establishment of DOE (Department of Energy)-Plant Research laboratory at the Michigan State University (MSU), designing its current building, and in the recruitment of the most successful plant biochemists in the world, a few to name: Anton Lang, Jan Zeevaart, Norm Good, Hans Kende, Peter Volk and Charlie Arntzen. It was Ed's vision and leadership that translated into one of the most successful plant biochemistry programs in the world at MSU.

Ed will always be remembered for his extreme love and dedication to Science. Scientifically, Ed thought big thoughts. He was worried about big scientific items – the air we breathe, the food we eat, and the biological production and consumption of carbon dioxide and oxygen. He perceived that the carbon metabolism of the plant world regulated the CO_2/O_2 balance of the atmosphere. In the early 1970s, the discovery of plant-type peroxisomes, glycolate metabolism via peroxisomes (Tolbert et al. 1968; Kisaki and Tolbert 1969; Tolbert and Yamazaki 1969; Yamazaki and Tolbert 1970; Tolbert 1971), and the key plant enzyme ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco), were central efforts in Ed's laboratory with emphasis on its ratio of carboxylase (CO_2 uptake) to oxygenase (O_2 uptake) activities (Andrews et al. 1971, 1973; Lorimer et al. 1973). Soon after joining Ed's laboratory, I told him that I did not believe that glycolate dehydrogenase is present in the mitochondria. I could see that his face turned red, and he was quite upset, but he asked me to prove my hypothesis that chloroplasts are the primary site for glycolate metabolism. I started a long eight-year journey to prove it, yielding the last publication with Ed suggesting that chloroplast (via electron transport) are *'probably'* the primary site for glycolate metabolism, and the remaining glycolate is exported for further metabolism (Goyal and Tolbert 1996). Although we were convinced with the data, but he was very careful to include the word 'probably' because he wanted me to perform a few more experiments before we say it conclusively. These were the only experiments where he would stand next to me all day to 'watch-over-my-shoulder'. Ed published over 270 papers in peer-reviewed journals. He was elected to the National Academy of Sciences, in 1984, in recognition of his pioneering discovery of peroxisomes in plants, their role in carbon metabolism, establishing the C-2 oxidative photosynthetic carbon cycle, and the role and mechanism of Rubisco in photosynthesis.

In 1989, when Ed was approaching to become Emeritus Professor of Biochemistry, he was convinced that plants play a significant role in regulating atmospheric levels of CO_2 and O_2 (Tolbert 1992). Around this time he read Lovelock's book *Gaia* (Lovelock 1979). 'Gaia' is the concept of a self-regulation entity – a living earth. He used to tell me how he can write 'Rubisco' all over in the book to describe the concept that "the atmosphere is not merely a biological product, but more probably is a biological construction – a living system designed to maintain a chosen environment". Therefore, he requested the organizers, of a 'transition to working retirement' symposium to be held to celebrate his accomplishments, to invite a few non-photosynthetic experts in the area of geology, geophysics, geobiochemistry, paleochemistry, ecology, environmental sciences, oceanography, marine mineralogy and marine biology to address historical and current viewpoints beyond the concept of global carbon cycle. On the last day of the symposium, he proposed a comprehensive hypothesis on how plants play a dominant role in the regulation of atmospheric levels of CO_2 and O_2. Ed also proposed that the term 'C-2 oxidative photosynthetic carbon cycle' parallel the nomenclature for the 'C-3 reductive photosynthetic carbon cycle'. Therefore, according to him, the term 'photorespiratory carbon cycle' should not be used for the C-2 cycle, because that implies photorespiration is a separate process with separate CO_2 and O_2 pools. Rather, there is only one process of photosynthetic carbon metabolism that is the sum of the C-2 plus C-3 cycles. The proceedings of the 'transition symposium' were published by the Oxford University Press, titled *Regulation of Atmospheric CO_2 and O_2 by Photosynthetic Metabolism* (Tolbert and Preiss 1994). At the conclusion of the symposium, Ed was determined to test his novel concept of Oxygen Compensation Point similar to CO_2 Compensation Point in plants and algae. I do recall that Ed tried to convince me to initiate research on the oxygen compensation points, but I had too many 'irons in the fire' as Ed used to say. The next year, he traveled to Germany to present his thoughts and convince many photosynthesis researchers to consider joint collaboration. Ed felt 'honored' that he was able to initiate a significant collaboration with Prof. Erwin Beck that yielded the first proof that oxygen compensation point exists in plants (Tolbert et al. 1995). In 1995, Yoshi Shiraiwa and I agreed to initiate research on this topic in aquatic green algae.

After the publication of the paper with Erwin Beck (Tolbert et al. 1995), he devoted all of his time developing the concept of oxygen compensation point, planning for a workshop with Barry Osmond and writing a major review/monograph. Three days before his untimely death, he shared with me, in a two-hour long telephonic discussion, his current thoughts, proposed several experiments and his frustration that journals declined publishing his manuscript, and how people are not able to understand the concept. I tried to convince him that the review was too long and complicated, and this is probably the reason why the journals were reluctant to publish it. Therefore, I suggested that instead of trying to publish a 100-page long typed review, he might consider publishing it as a monograph and send a copy to all photosynthesizers and scientists in other fields who may be interested in the subject. At the end of our conversation, he agreed to my suggestion, but told me that "You and Yoshi Shiraiwa need to get the data out".

Some of the significant research that Ed used to label as '*Eclectic*' yielded a major commercial product CCC (Cycocel). Royalty income from CCC was a major contributor to the early success of the MSU foundation that supports various research programs at MSU. In the late 1950s, he synthesized a compound that he never pursued because it killed plants (he showed me all the details and records in his data book). This compound glyphosate (commonly known as Roundup), a major herbicide, became a success story for the Monsanto Company in St. Louis, Missouri. The other significant eclectic research included enzymes for glycerol metabolism in plants and algae. I was also involved in this research. I do recall that when I was purifying DHAP (Dihydroxyacetone phosphate)-reductase, gradient tracings always showed a blip shoulder. On one TGTH (Thank God It's Thursday) afternoon, when our research group used to get together for informal drinks and research discussions, he challenged me with a '6 pack' offer to find another isoform of the enzyme. His persistence paid off; a new osmoregulatory isoform of DHAP-reductase was discovered (Gee et al. 1993). The osmoregulatory isoform of DHAP-reductase is specifically involved in the synthesis of glycerol. This was a great lesson to me to "view the data very carefully".

In 1997, Ed published a prefatory chapter for *Annual Reviews of Plant Physiology and Plant Molecular Biology* entitled the 'C_2 oxidative photosynthetic carbon cycle' (Tolbert 1997). Prefatory chapters are often filled with ramblings about one's life, but Ed dealt with the topic of himself only briefly. First, there was a half page chronological table at the beginning entitled 'Glycolate oxidase, glycolate synthesis, glycolate pathway and other related events of my life'. The first entry is for 1920 and it says simply: "Otto Warburg published that O_2 inhibited photosynthesis. That year, I was one year old in Twin Falls, Idaho." Then there is a short paragraph at the end: "This research occurred over a long period of time that was robbed from my family. I am most grateful to them for tolerating my single-minded devotion to it, which remains my only work and hobby. In the first draft of this chapter, I tried to mention names and results of all graduate students, postdocs, and visitors, who did the work. The review was far too long. For each of these associates our paths ran together for a valuable time, and I am forever grateful."

Ed was major professor for 28 graduate students, 49 post docs and visiting scientific associates. A few awards to name (included but not limited to): Fullbright fellowship, MSU-Distinguished Professorship, ACS (American Chemical Society) Spencer award, ASPP (American Society of Plant Physiology) Stephen Hales award, 1000 Most Contemporary Scientists (1981–1983), President of the ASPP, National Academy of Sciences (1984), Chairman, President's Blue Ribbon Panel considering Effect of Increasing Atmospheric CO_2 on Photosynthesis, Michigan Scientist of the year (1985), Humbolt Foundation Senior Scientist Award and Sigma Xi Scientist of the year (1990).

Ed will always be remembered by his graduate students, post docs and visiting associates as a very friendly and humble colleague, who never acted like a 'Boss'. He always gave more credit to his researchers than was really due. Ed will be remembered as a loving husband, and a father who conceded that he robbed a significant family time to perform his 'first love'. His wife Eleanor will probably attest that Science always came first in Ed's Life. Ed is survived by his wife Eleanor, his children David, Helen, Carol and Jim, his brother Bert, his sister Marian Childs, and his grandchildren Nicholas, Stephanie and Sarah.

Although Ed is not physically present with us, his vision will continue to show us new paths in photosynthesis research. Ed's students, close associates and plant biochemists who were either born through his vision of plant biochemistry at MSU or followed leads from his research contributions will always remember the most gentle and one of the most dedicated scientists they have known. Ed's presence at Plant Biochemsitry/Photosynthesis Conferences will be sorely missed. We all owe him for his contributions to photosynthesis research and for establishing fundamentals that will be explored in years to come.

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