



Nathan E. Tolbert

1919–1998

BIOGRAPHICAL

*Memoirs*

*A Biographical Memoir by  
Maarten J. Chrispeels*

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# NATHAN EDWARD TOLBERT

May 19, 1919–December 13, 1998

Elected to the NAS, 1984

Nathan Edward (Ed) Tolbert was a biologist widely known for his work on carbon metabolism in photosynthesis. He discovered the glycolate pathway and explored the role that peroxisomes play in this pathway and in photorespiration, the light-driven oxygen consumption and carbon dioxide emission of plants and algae. Toward the end of his career he developed the concept of the oxygen compensation point, the effect of atmospheric oxygen levels on photosynthesis by land plants and oceanic algae. He trained a large number of graduate students and post-docs, had numerous visitors working in his laboratory, and contributed substantially to the development of biochemistry at Michigan State University.



*N. E. Tolbert*

By Maarten J. Chrispeels

## Early life

Ed Tolbert was born on May 19, 1919 in southern Idaho. He was the oldest of four children of Edward, a farmer and businessman in southern Idaho, and Helen Mills Tolbert. As a boy Ed carried out the chores that the children of farmers were expected to do. Ed and his siblings grew up during the Great Depression, but the family managed quite well on the farm.

Ed's mother was a graduate of Grinnell College (1911) and had a Master's degree from the University of Chicago. She made sure that all her children went to college. Three out of four eventually became University professors. Ed attended a small elementary school, but his formal education was supplemented by his mother's attention to her children's intellectual needs. He attended Twin Falls High School and graduated in 1937. He then enrolled at Idaho State University in Pocatello, Idaho, where he majored in chemistry.

After two years, at the urging of his mother, he transferred to the University of California Berkeley. She had heard that it was a great place to study chemistry. Ed graduated from

Berkeley in 1941 with a BS degree in chemistry. His senior thesis was the light activation of silver halides.

After graduating college, Ed took a position at the University of California, Davis in the Department of Viticulture and Enology. There he worked with Maynard Amerine, and outstanding viticulturist and one of America's great wine connoisseurs. Ed published several papers on acidity and tannins in grape extract and wine. He also imbibed the finer points of wine appreciation from his mentor, with whom he shared living quarters. It was during this two year period he made his decision to pursue plant biochemistry, though World War II would temporarily interrupt this plan.

### Glycolate metabolism

In 1943 Ed enlisted in the U.S. Air Force for officer training as a photographic expert, a natural choice given his research at U.C. Berkeley on silver halides. After receiving training as a photo intelligence officer he had several assignments in the U.S. and then was sent to the Pacific theater as the allied forces tried to recover the Philippines and other Pacific islands. After recovering in Australia from a muscle wound in his leg that earned him a Purple Heart, he returned to the Pacific and went on to become part of the occupation force in Japan.

During his military service Ed realized that to be a more qualified researcher as a plant biochemist he had to get a doctoral degree. The GI bill helped make this possible for him as for so many others of that cohort whose studies were interrupted by serving their country in the war effort. The University of Wisconsin in Madison was then one of the premier places in the country to be trained in biochemistry. This was the subject that had initially sparked Ed's imagination while studying at U.C. Berkeley (but in which he received his lowest grade) and then became cemented during his time at U.C. Davis with Amerine.

At Wisconsin, Professor Robert Burris was his mentor. Bob Burris, a plant biochemist par excellence, had many interests and Ed worked on the light activation of the plant enzyme which oxidizes glycolic acid. He graduated in 1950; glycolic acid and its role and fate in plant cells would continue to fascinate him for the next 40 years.

After graduating, he returned as a postdoc to U.C. Berkeley, the other premier place for plant biochemistry in the 1950s. He was fortunate to work in the laboratory of Melvin Calvin. Others in the Calvin lab included Andy Benson and James Bassham, working

on elucidating the path of carbon in photosynthesis using  $^{14}\text{C}$  carbon dioxide and paper chromatography to separate the labeled compounds.

Glycolate was an early labeled compound during photosynthesis, but did not appear to be part of the immediate carbon assimilation pathway. Calvin, however, was concerned that the oxygen produced in the light reactions was somehow involved in carbon metabolism. Since Ed had worked on glycolate oxidation/ glycolate oxidase with Burris, he was tasked by Calvin to determine if oxygen produced by the light reactions was involved in metabolism of glycolate, phosphoglycolate, xylulose-5-phosphate and sedoheptulose-7-phosphate. These compounds were labeled within seconds after administering  $^{14}\text{C}$  carbon dioxide to algae or leaves.

Ed's results showed no role for oxygen in what was to become the Calvin-Benson cycle metabolism, so Calvin had no further interest and told Ed he could take glycolate metabolism for his own interest.

### **Early experiments with $^{14}\text{C}$ labeled compounds**

Robert Rabson, from the Atomic Energy Commission(AEC) that supported Calvin's lab, was a frequent visitor to the lab and told Ed of a position at the AEC. After finishing his one-year postdoc, Ed took a job with the AEC in Washington DC, evaluating grant proposals and committing research funds. He managed to find time to moonlight at the U.S. Department of Agriculture in Beltsville to study the light activation of glycolate oxidase in etiolated leaves.

In an important paper written with Marjorie Cohan, he showed that glyoxylic acid, the product of glycolate oxidation, is converted to glycine, serine and an unknown, when barley or wheat leaves are fed labeled glycolic acid.

After two years Ed returned to research full time and accepted a position at the Oak Ridge National Laboratory in Tennessee. The Oak Ridge nuclear reactor was the source of  $^{14}\text{C}$  labeled carbon dioxide, which, when fed to plants or algae, would find its way into many carbon compounds that could then be isolated and fed to plant cells to examine how they were utilized.

Carbon compounds were purified, broken down one carbon atom at a time to see which carbon atoms were labeled and how "hot" they were. At Oak Ridge he collaborated with Aubrey Naylor, Robert Rabson, and Al Haber, among others. Working with Pete Zill, he found that cultures of Chlorella fed  $^{14}\text{CO}_2$  would excrete labeled glycolate and

that the labeled glycolate in the medium accounted for 95% of all the excreted labeled compounds.

In June of 1952, Ed married Evelynne Cedarlund. Their two daughters, Helen and Carol, were born at Oak Ridge. Soon after, the family moved to East Lansing, Michigan, where they had a son, James, in 1960. Unfortunately, Evelynne passed away in December 1963, leaving Ed to take care of his three young children. In the summer of 1964, Ed married a widow, Eleanor Dalglish.

### Establishing the glycolate pathway

In 1957, Michigan State University (MSU) charged Dr. R. Gaurth Hansen with forming a biochemistry department in its College of Agriculture. Dr. Hansen brought together a core of MSU faculty and made a number of new hires. He wanted to have a good plant biochemist, and in 1958 he invited Ed to leave Oak Ridge and join his new department at MSU. Ed would rather have gone “out West” but the promises MSU made him—that he would be able to have graduate students, and that MSU would soon build a new building—convinced him that this would be an attractive move.

As it turned out, for the next 40 years, his entire academic career, Ed stayed at MSU. Little did he know that he would have to take out precious time from research to help design the new building and oversee its construction.

After Ed arrived at MSU, he pursued a number of research topics. Several people at Oak Ridge had been working on plant hormones, and Ed started working on the mode of action of the gibberellin antagonist (2-chloroethyl) trimethylammonium chloride and other quaternary ammonium compounds. The idea was to modify plant growth for the benefit of agriculture. Some of this work was done in collaboration with Sylvan Wittwer, his colleague in the Department of Horticulture. With A. A. Kahn he published several papers on breaking the dormancy of lettuce seed.

He was also involved in designing the new biochemistry building for the MSU campus. In spite of these research and administrative distractions he managed to continue work on photosynthesis and glycolate metabolism. When still at U.C. Berkeley, Ed contributed to establishing phosphoglycolate as one of the earliest compounds to be labeled. The research carried out at MSU and elsewhere in the early 1960s established the glycolate pathway. Ed’s research benefited from help of his brother Bert Tolbert, who had also become a chemist. Bert was at U.C. Berkeley where he synthesized the 1- and 2-[<sup>14</sup>C] glycolate that Ed used for his metabolic studies.

In 1961, Richardson and Tolbert described a phosphoglycolic acid specific phosphatase in the chloroplasts, suggesting that phosphoglycolate may be the source of glycolate. A paper in 1962 with Bob Rabson, added more details to the glycolate pathway. They used glycolate, serine and glycerate labeled in specific C atoms, and then examined the products and determined which carbon atoms were labeled and to what extent.

Another study in 1962 with P. C. Kearney showed that labeled phosphoglycolate and glycolate were released by isolated chloroplasts incubated with  $^{14}\text{CO}_2$ . They postulated that it was then oxidized by glycolic acid oxidase in the crystal and that the product (glyoxylate) re-entered the chloroplasts to be converted to serine and glycine. In 1965 Ed went on sabbatical leave to Freiburg (Germany) to work in the lab of Helmut Holzer, who was an expert on transketolase. Using a Warburg respirometer, they studied the uptake of oxygen by isolated chloroplasts upon the addition of either phosphoglycolate or glycolate.

Ever since the discovery by Otto Warburg in 1920 that increasing the eternal oxygen concentration inhibited photosynthesis in Chlorella grown in closed vessels under high light intensity, plant biochemists had studied photorespiration, light-driven oxygen consumption and carbon dioxide emission of plants and algae. What were the biochemical reactions of this process and why was it occurring? Evidence from a number of laboratories, including Tolbert's, showed that this was a universal process in plants and algae and that glycolate production was associated with photorespiration. The release of carbon dioxide in photorespiration was thought to be the result of glycolate metabolism, but the source of the glycolate and the ultimate fate of its carbons were unknown.

The field of photorespiration challenged many researchers because it was thought to be a wasteful process. It was suggested that if plants did not have photorespiration they would be more productive. Indeed, the plants such as maize and sugarcane with  $\text{C}_4$  pathway of photosynthesis described by M. D. Hatch and C. R. Slack in 1966, have no photorespiration and are generally more productive.

Ed's experience in designing research buildings landed him another job. MSU had won the competition to host a major new facility for plant research funded by the Atomic Energy Commission (AEC), and Ed was asked to "lend a hand" in designing the new

The field of photorespiration challenged many researchers because it was thought to be a wasteful process. It was suggested that if plants did not have photorespiration they would be more productive.

facility and shepherding it through the campus administration. He did a great job and it was a feather in his cap that the new AEC Plant Research Laboratory, as it was to be known, got off to an excellent start in 1966, with Anton Lang as the director.

### Isolating peroxisomes

In 1954 J. Rhodin introduced the term “microbody” to describe organelles with a single limiting membrane and a fine granular internal structure present in mouse kidney cells. Subsequently such structures were found in other mammalian cells. A few years later the work of Christian de Duve and collaborators showed isolated particles that resembled these structures to contain various oxidases, uricase and catalase.

In 1965 de Duve suggested the name “peroxisomes” for these particles because of their postulated important role in the breakdown of hydrogen peroxide. A study by H. H. Mollenhauer and his associates published in 1966 showed that many different plant cells and algae contained similar structures, which they called “cytosomes.” About this time, Christian de Duve came to MSU and gave a seminar about peroxisomes.

After attending the seminar, Ed came back to the lab and talked excitedly about the possibility that such particles also existed in plant cells and possibly contained glycolate pathway enzymes. Could his lab crew isolate such particles, he wondered?

Some time later, in May 1967, Harry Beevers gave a talk at the symposium held to celebrate the official opening of the AEC Plant Research Laboratory. Beevers reported on the success of his postdoc Bill Breidenbach in isolating particles from castor bean endosperm that could be separated on isopycnic sucrose gradients from mitochondria and banded at a density of  $1.25 \text{ g/cm}^3$ . These particles, which they called “glyoxysomes,” contained the enzymes of the glyoxylate cycle.

By this time Ed’s lab was already hard at work isolating peroxisomes from leaves. Isolating fragile particles from leaves presented its own challenges and required careful homogenization in buffered sucrose, sedimenting crude particle fractions, re-suspending the pellets gently and then partitioning the particles on sucrose step gradients.

The results showed that particles containing catalase, glycolate oxidase and DPNH (NADH) glycolate reductase traveled through 1.8 M sucrose but banded on 2.0 M sucrose. Cytochrome c reductase, a marker for mitochondria, banded on the 1.8 M sucrose layer. Electron micrographs showed these particles to be similar to the peroxisomes found in plant and animal cells. Two papers on plant peroxisomes, published

in 1968 and 1969, had four co-authors besides Tolbert, Angelika Oeser, a research technician from Germany, T. Kisaki, Richard Hageman, a sabbatical visitor from the University of Illinois, and R. K. Yamazaki, a graduate student.

In the next few years, Ed Tolbert's lab identified other enzymes in peroxisomes, demonstrated their existence in multicellular green algae, showed the role of peroxisomes in ureide biosynthesis in soybean nodules and established the appearance of peroxisomes in greening cotyledons of fat storing seeds. Being a consummate enzymologist interested in intermediary metabolism, Ed opened his lab to students and visitors, who also worked on quite a few other plant enzymes.

There was also a major effort on phosphatases, including 3-phosphoglycerate phosphatase by Doug Randall, and of course glycolate phosphatase, first by Randall and then by John Christeller, who joined the lab a few years later. Unicellular algae were found not to have peroxisomes but to oxidize glycolate slowly with a mitochondrial glycolate dehydrogenase.

Tolbert did not confine his work to plants and algae, but continued his work on peroxisomes in mammalian tissue. In 1981 he wrote a major review for *Annual Reviews of Biochemistry* entitled "Metabolic pathways in peroxisomes and glyoxysomes that covered plants, algae and animals."

Intellectually, though, the challenge remained understanding the source of glycolate and the role of peroxisomes in photorespiration.

### Rubisco activity, the source of glycolate

The work on peroxisomes brought Tolbert the recognition he deserved, but important intellectual challenges remained. What is the source of glycolate and what is the role of peroxisomes in photorespiration? Many plant biochemists worked on photorespiration in the 1970s and there were at least three proposals concerning the source of glycolate.

The holy grail was to increase photosynthetic efficiency by abolishing photorespiration, and the whole field was quite contentious in part because of the personalities involved. One proposed mechanism, discounted by the Tolbert lab based on experimental evidence, was that glycolate arose by an as yet undiscovered reductive condensation of two molecules of carbon dioxide.

The other proposal suggested that phosphoglycolate was formed by the oxidation of a phosphorylated intermediate of the photosynthetic carbon cycle. This led T. J. Andrews,

a postdoc, and G. H. Lorimer, a PhD student, in the Tolbert lab, to investigate (using [ $^{18}\text{O}$ ]-oxygen) whether molecular oxygen becomes incorporated into serine and glycine, the downstream products of the glycolate pathway. They found that it does, that this only happens in the light, and that the hydroxyl group of serine was not labeled. This was consistent with the oxidation of a phosphorylated intermediate.

The same year, 1971, George Bowes, Bill Ogren and Richard Hageman, who had worked with Tolbert on the isolation of peroxisomes, published a short article showing that purified soybean ribulose bisphosphate carboxylase catalyzes the formation of phosphoglycolate in an oxygen dependent manner. They found that  $\text{O}_2$  was a competitive inhibitor of the carboxylase reaction and measured the  $K_m$  ( $\text{CO}_2$ ) and the  $K_i$  ( $\text{O}_2$ ).

The Tolbert lab quickly confirmed those results using soybean carboxylase generously supplied by the Ogren lab. This resulted in the publication of two major papers by Andrews, Lorimer, and Tolbert in *Biochemistry* in 1971. They exhaustively characterized the reaction products and the conditions that permit the enzyme to be a carboxylase and/or an oxygenase. Eventually the name of the enzyme was shortened to Rubisco, where the last two letters stand for carboxylase/oxygenase.

In the next 15 years, the Tolbert lab published more than 20 research papers (and a few reviews) on Rubisco, dealing with its presence and properties in green algae, regulation by phosphate esters, active site studies with pyridoxal 5'-phosphate, changes in the abundance of the enzyme during plant development, the effect of glyoxylate on enzyme activity, the characterization of an active site peptide, the effect of triacontanol, a stimulant of plant growth, and certain post translational modifications of the protein.

They found that the N-terminal amino acid of Rubisco is acetylated. Ed's PhD student John Pierce collaborated with John Barker to make specifically labeled substrates and then studied the interaction of Rubisco with transition state analogs of ribulose 1,5-bisphosphate. They proposed a model for the carboxylation reaction of Rubisco that included a role for  $\text{Mg}^{2+}$  in the stabilization of the intermediate 2-C-carboxy-3-ke-to-D-arabinitol 1,5-bisphosphate.

### The Great Barrier Reef expedition of 1973

By the late 1970s the photorespiration debate had been settled by the isolation of phosphoglycolate phosphatase mutants of *Arabidopsis* by Chris Somerville.

These mutants could live and grow in 2% oxygen, but air, with 20% oxygen, was lethal! It was clear that abolishing photo-respiration was not an option to raise plant productivity.

During the mid- to late 70s, Tolbert became more and more interested in photosynthesis and photorespiration by algae in the ocean. Unicellular algae appear to have the enzymes of the glycolate pathway, and Pete Zill, working in Ed's lab in 1956 at Oak Ridge had shown that algae secrete glycolate. Is this glycolate a resource for other organisms in the ocean? Ed teamed up with Andy Benson, whom he had worked with in Berkeley but was now at the Scripps Institution of Oceanography at the University of California San Diego and Barry Osmond from the Australian National University in Canberra. Together they organized a grand expedition to the Great Barrier Reef.

They used the R/V Alpha Helix from Scripps and the modest shore laboratories at Lizard Island for their experiments. The participants consisted of 12 U.S. and 12 Australian scientists. The results, published in Volume 3 of the *Australian Journal of Plant Physiology*, showed that various species of algae in the various species of algae in the ocean do have photorespiration, but the level of glycolate in ocean water was much lower than they had hoped for, although several new marine photosynthetic organism were identified by the expedition members. Nevertheless, the well-attended discussions they had on the beach each night were extremely stimulating and productive.

Ocean water is low in CO<sub>2</sub>, so do algae concentrate it at the site of carboxylation, just like C<sub>4</sub> plants? Algae from the oceans being difficult to work with, Ed's postdoc James Moroney started working on carbon concentrating mechanisms in *Chlamydomonas reinhardtii* and the role of carbonic anhydrase in this process. That *Chlamydomonas* has such a mechanism was proposed in 1980 by R. M. Badger working in J. A. Berry's lab at the Carnegie Institution of Washington. M. H. Spalding, R. J. Spreitzer and Bill Ogren showed in 1983 that *Chlamydomonas* mutants deficient in the concentrating mechanism could readily be isolated. James Moroney and Ed teamed up with Barbara Sears from the Department of Botany and Plant Pathology at MSU to isolate similar mutants of *Chlamydomonas* that required elevated CO<sub>2</sub> for survival and showed that these were deficient in carbonic acid anhydrase. Subsequent research in Ed's lab demonstrated that *Chlamydomonas* has both a periplasmic carbonic anhydrase that is repressed by high CO<sub>2</sub>, and an internal one that is present under both low and high CO<sub>2</sub>.

## The oxygen compensation point

By the 1980s, Ed began to think of photosynthesis and photorespiration in a different way. He felt that the term photorespiration was a misnomer and should be replaced by the term “C<sub>2</sub> oxidative photosynthetic carbon cycle” as a parallel to the term “C<sub>3</sub> reductive photosynthetic carbon cycle” already widely used for carbon dioxide fixation. The C<sub>3</sub> cycle fixes CO<sub>2</sub> and emits O<sub>2</sub>, the C<sub>2</sub> cycle fixes O<sub>2</sub> and emits CO<sub>2</sub>. At ambient concentrations of O<sub>2</sub> (21%) and CO<sub>2</sub> (0.03%) the C<sub>2</sub> cycle consumes about 1/3 of the carbon fixed by the C<sub>3</sub> cycle. In 1987, Ed published a major review on this topic with David and Diane Husic, respectively a postdoc and PhD student in his lab.

The steadily increasing level of atmospheric CO<sub>2</sub> (the Keeling curve) and its effect on photosynthesis by land plants and oceanic algae entered our collective consciousness in the 1980s, and scientists working on photosynthesis began asking if this would increase yields of our crops, and how it would affect natural terrestrial and oceanic ecosystems.

The full extent of the effects of climate change was not yet realized at the time. Since increased CO<sub>2</sub> levels have the potential to increase crop yields of C<sub>3</sub> plants, whereas photorespiration decreases it, many plant biologists started working in this field. In 1983, Ed went to the 6th International Photosynthesis Congress in Brussels, Belgium, and gave a paper called “The Effect of Increasing Atmospheric O<sub>2</sub> on Photosynthesis.” The global picture—terrestrial and aquatic—became more and more part of his thinking.

In 1988 he received an Alexander von Humboldt Senior Scientist award and spent a year in Germany, first in Marburg studying the CO<sub>2</sub> concentration mechanism in *Scenedesmus* with Jens Thielmann, and then in Bayreuth with Erwin Beck. In Bayreuth they built an airtight chamber equipped with lights and gas analyzers to measure gas exchange with tobacco and spinach growing in different atmospheres (and levels of O<sub>2</sub>, especially). Ed and Erwin discussed the notion of an “O<sub>2</sub> compensation point.” The results were published much later in a PNAS paper. Retirement was just around the corner, and in 1989, when Ed was 70, he became emeritus professor of biochemistry.

A major symposium was held in his honor on the MSU campus. On the last day of the retirement symposium he presented his ideas about the O<sub>2</sub> compensation point and the role of photosynthesis in regulating the levels of O<sub>2</sub> and CO<sub>2</sub> in the Earth’s atmosphere to a sympathetic if somewhat skeptical audience. At the O<sub>2</sub> compensation point, net O<sub>2</sub> exchange would be zero given the light conditions and CO<sub>2</sub> concentration. During the evolution of our planet, O<sub>2</sub> concentrations had not always been 21%—the O<sub>2</sub> concen-

tration was 35% some 275 million years ago—and Ed wondered what impact this may have had on photosynthesis by C<sub>3</sub> plants. His experiments with Erwin Beck showed that the O<sub>2</sub> compensation point was 23% O<sub>2</sub> when CO<sub>2</sub> was 220 ppm, but rose to 35% O<sub>2</sub> in an atmosphere with 700 ppm CO<sub>2</sub>. At the 1995 level of CO<sub>2</sub> (350 ppm) the O<sub>2</sub> compensation point was 27%. (Tolbert et al, 1995.)

During the last few years of his life, Ed continued to refine his ideas about the O<sub>2</sub> compensation point was. Arun Goyal kept his lab going even when Ed and his wife were spending the winter months in Florida. Goyal published a number of papers, including a study that documents an alternate route for the catabolism of glycolate. (Goyal and Tolbert, 1996). As Ed generated new ideas about the oxygen compensation point he urged Goyal and his two collaborators, Erwin Beck in Germany and Yoshi Shiraiwa in Japan, to test those ideas experimentally.

### Honors and awards

Several important honors also came Ed's way in the 1980s. In 1981 he received the Stephen Hales Award from the American Society of Plant Physiologists (ASPP). In 1982 he became President-elect of ASPP, and President the next year. In 1984 he was elected to the National Academy of Sciences. In 1988 he received an Alexander von Humboldt Senior Scientist award and spent a year in Germany, first in Marburg studying the CO<sub>2</sub> concentration mechanism in Scenedesmus with Jens Thielmann, and then in Bayreuth with Erwin Beck.

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