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Remembering Tom Wydrzynski (1947–2018), one who had the guts to go after what he wanted and excelled at it

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ABSTRACT

We pay tribute to Tom Wydrzynski who passed away at age 71 on March 16, 2018, in St. Louis, Missouri, USA. He was a wonderful and caring human being, friend to many, and one of the great plant biologists/biochemists/biophysicists of our time. He successfully dug deeply into the function of the oxygen evolving complex (OEC) by applying a combination of novel biophysical and biochemical techniques to understand how plants produce oxygen from water. He then used this information to venture into artificial photosynthesis, a futuristic goal. In addition, Tom was the first to show that bicarbonate ions have a unique role to play on the electron accepter side of Photosystem II, water-plastoquinone oxido-reductase. This tribute draws heavily from the text that one of us (Govindjee) wrote in 2008 [1] and the unpublished text he read on behalf of many of Tom's friends on April 7, 2018, at a memorial service in St. Louis in celebration of Tom's life. This tribute is focused on Tom's time and work in Urbana, Illinois, but mentions other research as well. It ends with a fitting tribute, a poem written by one of Tom's contemporaries in Urbana, Ralph Schooley.

1. Introduction

Thomas (Tom) John Wydrzynski (Fig. 1) was the first child of Eva and Stanley Wydrzynski, born on July 8, 1947 in St. Louis, Missouri, USA. Tom received his primary and secondary education in St. Louis, graduating from Mehlville High School in 1965; he obtained, in 1969, his AB degree (cum laude in Biology and Chemistry) from the University of Missouri in St. Louis (UMSL). He then studied plant physiology, during 1969-1970, at Queen's University, Kingston, Ontario, Canada, before beginning his graduate studies in 1972 at the University of Illinois at Urbana-Champaign (UIUC), where he received his PhD in Biology in June 1977, while working with Govindjee. After his academic training in the USA, Tom worked in Europe and then in Canberra, Australia until his retirement. In 2011 Tom returned to his hometown in St. Louis. Tom Wydrzynski died peacefully on March 16, 2018 in St. Louis. He left behind his sister, Cynthia, two brothers, James & David Wydrzynski, and their families, in addition to many friends around the world who remember Tom fondly. A fund has now been established by his family and friends at the International Society for Photosynthesis Research (ISPR) in his honor; donations may be made by contacting Robert Burnap via e-mail: treasurer@photosynthesis-

research.org.

This tribute begins with a brief description of Tom's academic training in the USA, followed by his research life in Europe and then in Canberra, Australia, and the USA. We conclude with a few of the reminiscences received from friends and colleagues of Tom on the occasion of his 60th birthday (Govindjee [1]) and a few more received on his passing.

2. Tom's PhD days in Urbana, Illinois

Following the July 1972 visit to Govindjee's lab (277 Morrill Hall, Goodwin Avenue, Urbana, IL), Tom wrote "I am, of course, very much interested in your research in photosynthesis, and I am looking forward to the opportunity to work in your group this fall." R. G. S. Bidwell (an author of a popular Plant Physiology text) had written to Govindjee that "Tom has certainly guts to go after what he wants". Tom's teachers in St. Louis had described him as "intelligent"; "conscientious"; "written work always well thought out and completed on time"; and "one of the most industrious and conscientious students I have come across." Tom joined the UIUC PhD Program in Biology in 1972 under Govindjee's supervision. Tom touched the hearts of all of his professors and his colleagues in the

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Fig. 1. Tom Wydrzynski at UIUC, 277 Morrill Hall (photo taken in 1999).

laboratory. Figs. 2 and 3 show photographs of Tom with his colleagues. Tom's first project (1974–1975), in collaboration with Prasanna Mohanty (1934–2013; see Naithani and Govindjee [2]; Tiwari et al. [3]), was to investigate the role of magnesium and sodium in regulating photosynthesis. While Tom completed and published this work, it clearly was not his passion. However, he worked on this project with full vigor, even after 1975 (see Mohanty et al. [4], Wydrzynski et al. [5], and Govindjee et al. [6]). For a current view on this topic, see Kaňa and Govindjee [7]. Soon thereafter, Govindjee suggested to Tom that he might wish to solve the problem of precisely where "bicarbonate/ CO2" functions in the steps of electron transport from water to ferredoxin.

Although many studies had suggested that bicarbonate had an obligatory role in electron transfer in photosynthesis, its precise function was not understood. The 1931 Nobel laureate Otto Warburg, who had discovered this phenomenon, made the assertion that $\rm CO_2$ was the source of oxygen in photosynthesis [8]. Tom's breakthrough discovery in 1975 suggested that the site of bicarbonate function was not on the water oxidation side, but instead it was on another site involving

plastoquinone (Wydrzynski and Govindjee [9]; Khanna et al. [10]). This discovery led to further investigations in this area and inspired the PhD theses of many of Govindjee's other students: Rita Khanna, Julian Eaton-Rye, Danny Blubaugh, Jin Cao, and Jin Xiong; Govindjee continues to work on it even today! See a review by Shevela et al. [11] for details. Despite the considerable importance of his discovery, Tom considered the bicarbonate project as Govindjee's idea and felt that he had to have a problem that was his own—one that he had thought of himself. Tom was inspired to solve "how plants make oxygen" after attending a course taught by Prof. Paul G. Schmidt in the Department of Chemistry at the UIUC. He proposed the use of Nuclear Magnetic Resonance (NMR) to study oxygen evolution, something no one had done before in photosynthesis. Govindiee said to him "OK, but you are on your own". Tom convinced Nick Zumbulyadis, a postdoctoral associate in the lab of Herb Gutowsky, a preeminent leader on NMR in Chemistry, to work with him; they were joined later by Steve Marks. With the crucial help of Zumbulyadis and Marks, Tom was the first to apply nuclear magnetic resonance relaxation measurements to probe the role of manganese in photosynthetic oxygen evolution. In the next three years (1975–1978), Tom was first author on three papers on what was learned from this innovative application of NMR to probe water oxidation [12-14]. Tom was the first to show that period 4 oscillations occur in NMR relaxation [20], which explains and is consistent with the period 4 oscillations in oxygen evolution, discovered earlier by Pierre Joliot, grandson of Pierre and Marie Curie. As a graduate student, Tom received a Public Health Service National Research Award during 1975-1977. His PhD thesis entitled "The Role of Manganese in Photosynthetic Oxygen Evolution" was accepted in 1977 with high recommendation by his doctoral thesis committee [Govindjee (chair); Charles Arntzen, Colin Wraight, and Paul G. Schmidt, members]. Tom dedicated his PhD thesis to his father Stanley Wydrzynski. He wrote: "In memory of my father, who gave me all that he could not - would not - have". For his thesis research, he received a first-place rating in the Sigma Xi student paper competition.

With time, Tom became an authority on *the water oxidizing system of photosynthesis, the one that makes oxygen for all of us.* Another of Tom's major achievements was the use of ¹⁸O isotope exchange measurements to probe the binding of the substrate water in the oxygen evolving complex. As follows below, Tom moved on to become one of the early pioneers of research on "artificial photosynthesis", an area important for developing clean fuels. Figs. 4 and 5 show Tom with several who had gathered at UIUC in 1999 at the time of Govindjee's retirement.



Fig. 2. Left to right: Tom Wydrzynski, Rita Khanna, and Paul Jursinic (1970s).



Fig. 3. Left to right: Rita Khanna, Daniel Wong and Tom having fun wearing different parts of the PhD graduation robe of Rita (May, 1980).

3. From Urbana to Australia, with exciting research in many labs en route

After holding a brief research position at Standard Oil of Indiana in Naperville, Illinois, Tom entered into highly intellectual interactions with top scientists from around the world, including Kenneth Sauer (University of California Berkeley, USA); Gernot Renger (Technical University, Berlin, Germany); Yorinao Inoue (RIKEN, Wako-Shi, Japan); Slava Klimov (Pushchino, Russia); and Tore Vangaard (Gothenburg, Sweden). In 1991, he settled down as a Professor in the Department of Biological Sciences at the Research School of Biological Sciences (RSBS), Australian National University (ANU), in Canberra, Australia.

Fig. 6 shows Tom with friends at 10^{th} International Photosynthesis Conferences in Montpellier, France, 1995.

At RSBS, Australia, Tom built a stellar, internationally recognized career. This happened because Barry Osmond (Director-Elect of RSBS, ANU) had noticed Tom's contributions to the understanding of photosynthetic oxygen evolution, and was highly impressed by his review on the mechanism of water oxidation by plants (Hansson and Wydrzynski [16]). Osmond telephoned Govindjee for his opinion of Tom and his



Fig. 5. Tom Wydrzynski in Urbana, Illinois, at the time of Govindjee's retirement in 1999. Left to right: Julian Eaton-Rye, Tom, Rita Khanna, Rajni Govindjee, Govindjee and Barbara Zilinskas.



Fig. 4. Left to right: Tom, Alan Stemler, Jin Xiong, Teruo Ogawa, Paul Jursinic, Maarib Bazzaz, Govindjee, Rita Khanna, Barbara Zilinskas, Jack Van Rensen, Mary Ann van Rensen, and Julian Eaton-Rye (Photo, 1999).



Fig. 6. Tom Wydrzynski with his friends at the 10th International Conference on Photosynthesis Research held in Montpellier, France, 1995. *Top row* (left to right): Bill Coleman, Julian Eaton-Rye, Christa Critchley and Alan Stemler. *Middle row* (left to right): Jack van Rensen and Danny Blubaugh. *Bottom row* (left to right): Tom, George Papageorgiou (sitting) and Govindjee.

research. Listening to the highest praise he had heard about any scientist, Barry Osmond offered Tom a faculty position at ANU. Tom served as a professor for 20 years where he mentored many students and postdoctoral associates until his retirement in 2011. The research of Tom and Johannes Messinger provided the first clear illustration of the nature of the binding sites of the two water molecules involved in oxygen evolution in photosynthesis (see Messinger et al. [17]; Wydrzynski et al. [18]). Those who followed this research included the late Warwick Hillier (1967–2014). (See Hillier et al. [19] and Hillier and Wydrzynski [20].) In addition, Tom collaborated with Ron Pace and Elmars Krausz on the basic chemistry of the intermediates of PSII, namely tyrosine, the Mn cluster, and a few other components of the oxygen evolving complex [21–24].

Tom's ultimate foray in research was the excitement he felt as he explored artificial photosynthesis with his ANU research team. Here, we cite his research on "efficient" electron transfer from a photo-pigment to a quinone (similar to that in Photosystem II of plants), both located within an engineered protein (Hay et al. [25]). After retirement, Tom returned, as mentioned above, to his hometown of St. Louis, Missouri in 2011, but he continued as a Visiting Fellow of RSBS until August 2017.

4. Reminiscences of Thomas (Tom) John Wydrzynski

Tom was clearly an internationally known scientist, distinguished author, and great mentor who had friends and colleagues scattered all over the world. We present below rememberences from his closest friends and colleagues who have remembered him over the years.

Fig. 7 shows Tom Wydrzynski at a gathering in Australia in 2005.

4.1. Comments received in 2008, at Tom's 60th birthday

In a tribute to Tom on his 60th birthday (cf. see [1]), the following scientists from Australia, Germany, India, New Zealand, Sweden, and the USA sent their comments: Lars-Erik Andreasson, Brendon Conlan, Charles Dismukes, Julian Eaton-Rye, Hans-Jo¨rg Eckert, Christiane Funk, Orjan Hansson, Sam Hay, Warwick Hillier (1967–2014), Brad Huggins, Paul Jursinic, Rita Khanna, Vyacheslav (Slava) Klimov (1945–2017), Elmars Krausz, Iain McConnell, Johannes Messinger, Prasanna Mohanty (1934–2013), Barry Osmond, Reza Razeghifard, Kenneth Sauer, Tore Vanngard, Haoming Zhang, and Barbara Zilinskas.

Below are some of the recollections from that time (for others, see [1]).

Johannes Messinger (Sweden), who had done exciting research with Tom, wrote "He is often underestimated in the field because of his

quiet and friendly nature. However, anyone who gets to know him on a personal level realizes quickly how immensely knowledgeable he is about the water-splitting system in photosynthesis. I also value that he thinks freely and unconventionally, not bothered by current trends in the field. He is extremely open to new, challenging ideas, and is willing to follow them up, even against negative predictions by others. I like to add that this strategy has been successful in many cases!"

Prasanna Mohanty (India), Tom's very first coworker, wrote "Here is my story of 1980 in Greece. I was very hungry and searching for a way to cash a twenty-dollar American Express check. Suddenly, Tom appeared on the scene and gallantly offered me as a loan, a 'five US dollar bill'. I have felt, over the years, not only the depth of his scholarship, but also his humanism. Each meeting with Tom had a beautiful feeling. Tom readily reveals the 'inside-out' of his personality, and no wonder, he from the outside easily peeps into the interior of the mechanism by which plants evolve oxygen. Thank you, Tom."

Kenneth Sauer (USA), Tom's postdoctoral advisor, wrote "Tom proposed, in 1980, that during a specific key transition of the so-called 'oxygen clock', bound water becomes partially oxidized, rather than a further increase in Mn oxidation. This ingenious and highly original work was little noted at the time. To my mind, this is an outstanding example of a creative imagination supported by sound chemical thinking at work."

Tore Vanngard (Sweden) remembered: "Tom worked with us from April 1986 until April 1988. By the time Tom came to us, the mechanism of oxygen formation in PS II was largely unknown. Together with Jonas Angstrom, Tom found that hydrogen peroxide was produced under conditions when oxygen formation was hampered, which had some key implications for the underlying mechanism (Wydrzynski et al. 1989 [26]). It was a great pleasure to work with Tom. He certainly became a good friend to all of us!"

Brendon Conlan (Australia), a student of Tom, wrote "Tom looks after his students well and is keen to associate with them outside of work hours. We often have video nights or beer and pizza nights at Tom's place, and Tom is renowned for putting on the best snacks menu around. So much so that rarely can anyone eat any of the pizzas ordered."

Julian Eaton- Rye (New Zealand), a fellow graduate student at the UIUC from early days, wrote of his visits to Canberra: "Tom has always been a great host—putting me up in his home and making sure no visit goes by without a chance to visit the surrounding countryside."

Slava Klimov (Russia), a scientist from Pushchino, described Tom as a "highly intellectual and friendly man, very pleasant in both scientific and social discussions."



Fig. 7. Tom Wydrzynski standing on the left in Canberra, Australia, with his friends and coworkers, at a 2005 Christmas party of the Photobioenergetics Group, Research School of Biological Sciences (with guests from the Research School of Chemistry), Australian National University. Front row (from left to right): Fred Chow, a student, Warwick Hillier holding Henry Oliver Hillier, Adele Williamson, Eun-Ha Kim, Ting Chow, Dayong Fan and Pui San Chow. Back row: Hossein Fallahi, Javier Fernández-Velasco, Joe Hughes, a student, Iain McConnell, Zhi-Ren Chow, a student, Cornelia Osmond, Barry Osmond, Jan Anderson. Photo taken by Elmars Krausz at Cotter Dam.

4.2. Recollections received in 2018 after Tom's death

Here are some of the recollections received after Tom passed away. **John Boyer**, a professor of plant physiology at UIUC, wrote "We knew Tom not only from Illinois, but also in Australia during one of our many visits there. He was a good thinker and always a friend."

William Coleman wrote "It is a terrible shame that Tom passed away. The last contact I had with Tom was when I visited him in Berlin in May, 1989, just before the Berlin Wall fell. I'm sure if it hadn't been for Tom, I might never have gotten interested in using Nuclear Magnetic Resonance for studying photosynthesis."

Paul Jursinic's description of Tom, in 2008, had included phrases "cheerful and insightful"; "one who has quick understanding of experiments carried out by others"; and "one who is always generous with his suggestions, and who has positive criticisms". Paul wrote "Tom always mastered experimental details and strived to give unbiased and globally applicable interpretations of his results. He could move beyond his own point of view, which I later appreciated to be a unique trait." Recently, Paul added "I was sorry to hear the news of Tom's passing. I do remember him fondly since we were in graduate school at the same time. He was for me a trusted colleague who introduced me to doing experiments with "magnetic resonance" that ended up in my thesis. We shared quite a few cups of coffee and donuts and ideas about photosynthesis and even about life. Tom's enthusiasm for experiments was infectious and it really brought an element of fun and excitement to long hours of work. As I think of Tom, the word that continues to come to my mind is "humility"- an ideal colleague: extremely intelligent, self-effacing, hardworking, honest, and a genuinely nice person. The years I spent doing research on photosynthesis were greatly enhanced by the friendship and scholarship shared with Tom. We miss you Tom!"

Rita Khanna wrote "A fond farewell to Tom, who will be missed by all who came to know him. Tom was a very special person and I feel very fortunate to have met him when I came to Govindjee's laboratory in 1974. Tom's love for science not only defined him but was also a source of inspiration for me. He was a true friend who cared deeply about others. He was full of life and besides his love for science, his interests extended to so many different facets of life including travel, music, cooking and just having fun. He will be remembered and cherished for his friendship, kindness, compassion and good humor. Tom touched us all and he will be missed, honored and long remembered." Rita added "The real friendship is like fluorescence, it shines better when everything is darkened."

Paul G. Schmidt wrote "During his Ph.D. studies with Govindjee, Tom Wydrzynski organized a project involving my lab and others at the UIUC Chemistry Department. I remember him for his enthusiasm for the

novel studies and his independent management of the project. He was a positive and warm person whom I enjoyed talking with."

David VanderMeulen wrote "I have fond memories of Tom as a kind and caring collaborative member of the 'Govindjee team'. He demonstrated the commitment to make a difference by doing a thorough job in planning and performing his project tasks with excellence. Tom will be missed."

Daniel Wong wrote "Tom and my paths through life met for over five years in the 1970s. We shared similar life struggles as fellow graduate students at the University of Illinois at Urbana-Champaign. Together with our contemporaries in Govindjee's laboratory, we formed a tight-knit group providing friendship and support for each other. I remember Tom arriving every morning bright eyed and bushy tail ready for the adventures of another day. Most memorable were our social gettogethers, cooking at Tom's apartment, and sightseeing trips to Chicago, St. Louis, and the Ozarks. I remember Tom as a kind, humble, and cheerful friend who was always willing to lend a helping hand. Tom has now taken the step to a better place. Good-bye, Tom! I will hold the memory of your characteristic smile with me."

Barbara Zilinskas: In 2008, Barbara had written "Tom struck me then, when I was a student in Govindjee's lab, as a serious and creative student who was bent on tackling an important problem with all the intensity that it deserved. He was quiet and shy, but Rita Khanna and I worked hard to loosen him up and involve him in the many shenanigans we would concoct. Over those two years in Urbana, I learned that Tom was not only talented and clever but he was also kind and compassionate." She added in 2018 "I have a heavy heart as I write to you. Tom was a wonderful friend to all those who had the good fortune to know him. We shall sorely miss his kind and caring spirit. I remember fondly the occasions when my cohort of graduate student "sisters and brothers" found comfort and peace in difficult times simply by knowing that we were part of a closely-knit family away from home. So, I'm very sad to learn that we have lost another beloved member of our lab family - Tom who follows Prasanna (Mohanty). Their contributions to our knowledge about the intricacies of photosynthesis are immeasurable, and the joy that both of them brought to their friends and colleagues is also priceless. Today (March 25) is Palm Sunday for Christians around the world. It marks the beginning of Holy Week, a very sad week that culminates next Sunday (April 1) in the joyous Easter. I am glad to be a Christian, and through my spiritual beliefs, I find solace in knowing that Tom and Prasanna are at peace in Heaven. I would be surprised if they didn't find a quiet table where they were discussing their latest ideas about photosynthesis over a good cup of coffee. Let there be Peace."

Nicholas (Nick) Zumbulyadis wrote: "I arrived at the UIUC fortyfour years ago as a post-doc in Herb Gutowsky's lab looking for a

project to define the next segment of my professional life. I had done my dissertation on liquid crystal NMR and was hoping to do something related, perhaps in the area of biological membranes. At the time NMR was not the big business that it is today, and most of the advanced methods we take for granted today did not exist. The equipment was mostly home-built, or worse yet, legacy spectrometers dating to a time when NMR was at its infancy. And then, Tom showed up in my office! He described a project which involved NMR and membranes and on top of that, photochemistry. Even today using NMR to monitor a photochemical/photobiological process in situ is a very specialized field. The project had everything I was hoping to get involved with. He explained to me the theory behind what he was proposing. It was not run-of-themill NMR, and I had to double-check my NMR textbooks to make sure it was possible. I looked at my equipment, which we would certainly be pushing to its utmost limit. We talked some more, decided to give it a try, and we did; the rest is history ...!"

In addition to this tribute, Brendon Conlan, Govindjee, and Johannes Messinger have just corrected the proofs of another one, which is in press, in *Photosynthesis Research*: "Thomas John Wydrzynski (8 July 1947 - 16 March 2018)"; it focused on Tom's extensive research in Australia. See https://doi.org/10.1007/s11120-018-0606-9 at Photosynthesis Research.

5. Tom's editorial activities

Tom's highly successful edited volume on Photosystem II (Wydrzynski and Satoh [15]) remained the bible in this field for years. We would also like to mention a wonderful educational review Tom wrote in 1981 (Wydrzynski [27]) and his contribution to editing a special issue in a journal [28].

6. Farewell

We end this tribute with a poem recited by Govindjee at the memorial celebration of Tom's life on April 7, 2018. This heartfelt poem entitled "Enchanting and True" was written by Ralph Schooley, one of Tom's contemporaries and friends in graduate school days.

Tom

Listen and hear Of memories captured That some revere As heightened rapture. A time with Tom with research so vast, What was it like? Hear my words, at last, Youthful enthusiasm abounded A time to think and ponder A new experiment resounded That kept us thinking of vonder. On our way to a conference A Howard Johnson's on the highway Let's eat with confidence Best to stop before taking the byway. The lab was a place to pleasure Plants below and sky above Beauty beyond measure No better place to love. Tom, you were a treasure Best to be found Tom, you were my true friend No better can be Now I can feel you Right here in my heart Now I can hear you Right here in my soul Now I can see you Right here in my mind Oh! How I miss you

Tom is gone. We all miss him and will cherish our memories of him forever. We also know that all those who have worked with Tom from around the globe will miss Tom dearly.

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