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Obituary

Seikichi Izawa (1926–1997)

On October 8, 1997, Seikichi (Sei) Izawa died at the age of 71. Sei was born on September 28, 1926 in Yokohama, Japan. Although he lived in the United States for most of his professional life, he always retained his Japanese heritage and citizenship with pride.

Sei went to high school in Mito, Japan and then took a baccalaureate degree in Plant Science from the University of Tokyo in 1950. He continued with graduate studies under the old system at the University of Tokyo Graduate School and graduated in 1955. During this period, Sei studied the mechanisms of glycolate and lactate oxidation in leaves (Izawa and Tsukamoto 1954). After graduation, he continued his studies of plant biochemistry by pursuing his Doctor of Science degree, earning it in 1961. During this period, Sei ran the first of the many Hill reactions which came to characterize his career (Izawa 1962). Thylakoid catalyzed Hill reactions and related electron transport reactions would become the major focus of his scientific interest throughout his academic career. This 1962 paper was on the stimulatory effect of CO_2 on the Hill reaction, a phenomenon that was discovered by Otto Warburg. The paper brought him scientifically close to the late Norman Good, who was also working on the same topic (Good 1963).

Upon earning his DSc degree, Sei took his first faculty appointment as an assistant professor in the Laboratory of Biological Chemistry at the Tokyo Institute of Technology in 1961. While there, Sei started to work with the hydrogenase reactions of *Rhodopseudomonas palustris*, but found a collaboration with Michio Itoh and Kazuo Shibata on thylakoid membranes to be more productive. Together, Sei and his colleagues did some early work with detergent fractionation, light induced 'shrinkage' and 'deformation' of thylakoids. After two years at the Tokyo Institute of Technology, Sei left Japan to accept a prestigious C.F. Kettering International Fellowship for Photosynthesis Research in the laboratory of Norman Good at Michigan State University. This fellowship started the long term collaboration between these two

outstanding scientists. Together, Sei and Norm Good began a productive study of thylakoid electron transport using salts, specific inhibitors, electron donors and acceptors. Many of Sei's most cited publications are characterizations of the ways in which specific molecules interact with the thylakoid electron transport process. In 1966, Sei was co-author of two publications (Izawa and Good 1966; Good et al. 1966) which were independently selected by Institute for Scientific Information as 'This Week's Citation Classic' appearing in Current Contents in 1987 and 1983, respectively. In the 1966 Izawa and Good paper, Sei published one of his few papers using electron microscopy (EM). When selected as a citation classic in 1987, this paper had been cited in over 325 publications. Sei had discovered a massive thylakoid swelling induced by light driven amine uncoupled electron transport and wanted to document this phenomenon with EM. Curiously, it was the dark control samples that led to Sei's discovery that granal thylakoids can unstack and then restack themselves in response to changes in media salt concentrations. Probably most of the citations of this paper have referred to these reversible unstacking/restacking controls.

It was during this collaboration with Norm Good that Sei began to study the stoichiometric relationship between ATP synthesis and electron transport (Izawa and Good 1968). This new direction led to a number of important papers during the 1970s wherein Sei documented the mols of ATP formed as two equivalents of electrons flowed through the photosynthetic electron transport proteins. Sei's studies, along with those of many other workers, provided strong evidence in support of the chemiosmotic theory of energy coupling.

Since Sei was a Japanese citizen who was in the US on a fellowship, his immigration status was problematical. So, in 1968, Sei moved to Kingston, Ontario, Canada where he became an Assistant Professor of Biology at Queen's University, temporarily obviating his immigration problems. Shortly after arriving in Canada, Sei married his wife, Toyoko. One year later, he was promoted to associate professor while continuing his studies of thylakoid electron transport.

From 1967 to 1974, Sei was a frequent summer visitor at Brookhaven National Laboratory where he collaborated with Geoff Hind. Sei's ingenuity was evident in the first of these 'summer fruits' – a paper on the kinetics of the pH rise in illuminated thylakoid suspensions. The authors used a flow cell approach to show that the lags and overshoots characteristic of pH rise profiles seen with conventional pH meters were instrument artefacts. The stoichiometry of proton uptake to linear electron flow was determined accurately for the first time and shown to be 2 H^+/e^-.

Otto Warburg's group had shown in 1946 that oxygen evolution by chloroplast fragments required the presence of chloride ion. In other work done at Brookhaven, Sei joined an ongoing study of the chloride requirement being done by Hind and Herb Nakatani. Their joint results established the basic properties of the chloride dependency (Hind et al. 1969). With this work and its later extensions (Kelly and Izawa 1978; Muallem and Izawa 1980; Muallem et al. 1981; Izawa et al. 1983), Sei became one of the pioneers who saw the critical role chloride ion plays in water oxidation long before it was hot research area.

After four years in Canada the immigration climate improved and Sei returned to the United States as an Associate Professor in the Department of Botany and Plant Pathology at Michigan State University. Now back in Norm Good's department, the Izawa and Good collaboration was revived. During the next few years, Sei published more work which has since been widely cited (for example: Ort and Izawa 1973, 1974; Izawa and Ort 1974). But, his position at Michigan State University was not a tenure track appointment and in the fall of 1974, Sei opted for more security and moved from East Lansing to Detroit, Michigan where he was appointed Professor of Biology at Wayne State University. He served Wayne State in this capacity for 22 years. At Wayne State, he continued his studies of thylakoid electron transport (Berg and Izawa 1976, 1977; Izawa and Berg 1977) but expanded his horizons by helping direct research on the effects of toxins on respiration in maize tissue (Bednarsky et al. 1977) and on the photoinhibition and glycolate excretion in *Microcystis aeruginosa*.

Sadly, Sei's academic career ended tragically just weeks short of his anticipated retirement. On a wet and snowy February day in 1996, Sei was running a few minutes late when he hurried to his Plant Physiology class where his students were waiting. There was snow melt by the door and when he entered the classroom he slipped, struck his head, and was sent to the emergency room in critical condition with a serious head injury. He lost his ability to walk and to talk. His recovery from this accident was slow, but he was making some progress. However, he never fully recovered and he did not return to work. In the spring of 1997, cancer was diagnosed and on October 8, 1997 we lost a fine scientist, colleague and friend.

Sei will be remembered as a master of innovation and creativity. He could always find a way of using that equipment which was available to make the measurements which he needed. He modified an old Beckman DU spectrophotometer for filtered actinic illumination and protection of the PM tube so that he could use the spectrometer for measurements of thylakoid fluorescence. He found some simple glass Geiger tubes which held 13 mL of liquid and then built a castle to hold the tubes out of discarded copper pipe and plexiglas. He machined the plexiglas to hold two pools of liquid mercury which served as the electrical contacts for the electrodes of the Geiger tubes. Once connected to a simple scaler, Sei could easily count the radioactive events associated with the ^{32}P-ATP synthesized by isolated thylakoid membranes. The ATP synthesis was measured in the same samples that were used to measure electron transport and so very precise P/2e ratios could be routinely obtained (Ort and Izawa 1974).

Sei will be remembered for his intense love of, and dedication to, science. His wife Toyoko will tell you that with Sei, 'Science always came first!'. This statement is certainly consistent with the Sei Izawa that I knew. In the fall of 1975, I started a postdoc with Sei, equipped with a fresh PhD only a few days old. The day that I arrived in his lab, his intensity was clear. He had already read all of my papers, preprints and my thesis and he had questions. Lots of questions. Questions relating my work to his. Questions relating my work to other labs. Didn't I think that my conclusions overreached the evidence? Wouldn't this alternate explanation work as well? What other evidence could be provided to support the conclusions? The questions continued for the two years that I worked with Sei and provided an invaluable addition to my scientific training. And, the questions continued for the other postdocs and graduate students. Sei had a reputation in the Biology Department at Wayne State for having a very keen intellect and for asking very probing, deep questions during seminars or when serving on graduate committees. But, Sei's science was more than questions. He also worked at the bench; every day! During the day, Sei could be found doing his own experiments or working with a postdoc or graduate student. When Sei did his independent experiments, he was usually repeating observations which served as the key experiments in a publication. Sei did not want to publish anything that could not be reproduced.

Sei will be remembered for his commitment to students and his dedication to his teaching. Many who put in as many hours on research as Sei did would let their teaching suffer, but not Sei. When his graduate students and postdocs went home for supper at the end of the day, Sei remained, working into the wee hours of the morning, preparing for his teaching. Sei had a folding chaise lounge (like those found on every patio) in his office. When he had a big lecture or teaching lab the next day, Sei would work most of the night preparing and then spend the last few hours sleeping on the old chaise lounge instead of going home. When the next day came, Sei was prepared to help his students to a better understanding of plant physiology.

Sei will be remembered as shy and humble man who avoided the limelight and much preferred doing experiments than going to meetings. He was quick to give others (postdocs, graduate students and undergraduates) more credit than was really due. But, the scientific community has long recognized his contributions to photosynthesis and to science. It is noteworthy that the Institute of Scientific Information cited Sei as one of the 'Most Cited Contemporary Scientists' in 1981 and that he was listed in 'Citation Classics' in the 1987 Current Contents.

Sei will be remembered as a loving husband and a father who was very proud of his daughter, Eri. While working with Sei, my first child was born. I would come to the lab and provide the kinds of progress reports that proud new dads always do. With my reports, Sei's eyes would always light up, he would smile, acknowledge my story and then have a fresh anecdote about Eri who was a few years older than my son. Usually, Sei's anecdotes provided evidence that Eri was an unusually gifted young lady. This preliminary evidence of Eri's ability was later confirmed when she graduated from MIT with a degree in physics, making her father immensely proud. Sei's dedication to Eri is manifest in that Sei once sacrificed a sabbatical leave in Japan to be home with her when he thought that she needed him.

The photosynthesis scientific community will miss Sei Izawa, one of the most gentle and one of the most dedicated of scientists we have known. Sei's contributions to photosynthesis were fundamental in establishing the utility of many electron donors, uncouplers and energy transfer inhibitors now in the toolbox of photosynthesis research. We all owe him a debt for placing them there with the guarantee that if Sei Izawa had studied it, the effects would be thoroughly explored and documented for posterity.

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