

## Thomas K. Hodges

### How did you spend your career?

As an undergraduate at Purdue University from 1954 to 1958, I majored in turf grass management, an option within the Agronomy Department. I wanted to become a golf course superintendent. I got a part-time job working for William H. Daniel, a turf grass specialist, and his graduate student, Norman Goetze. Dr. Daniel paid me \$0.60 per hour. One day, Norman asked me if I had considered going to graduate school, and I answered, "not really." This led to a long discussion about the importance of knowledge, education generally, research, and ways of contributing positively to the world. That discussion changed my life, because he convinced me I should go to graduate school and that I should go to an up-and-coming university located in Davis, California. Most of the professors had moved there from the University of California, Berkeley. He even suggested that I try to work with Robert Hagan, a turf grass irrigation specialist in the Irrigation Department.

I was accepted by the University of California, Davis, offered a research assistantship to work with Hagan, and was on my way to UC Davis in the summer of 1958. I entered the Plant Physiology Program, fell in love with UC Davis (the student body numbered about 3,000, and the town of Davis was about 6,000, as I remember). I met a young professor in the Irrigation Department, Yoash Vaadia, and he soon became my PhD supervisor.



Yoash was, and probably still is, the brightest person I had ever met. Yoash had a strong physical chemistry background, and he made me want to be better than him at something, so I concentrated on biochemistry. We had many debates, and I remember vividly the first time I bested him—that felt so good!

One of the courses I took at UC Davis was plant nutrition, taught by Emanuel Epstein. It was in this course that I was shocked to learn how little was known about the biochemistry of ion transport across cell membranes. If I had not already chosen a dissertation topic concerning long-distance ion transport in plant roots, I would have immediately approached studying the energetics of ion transport across cell membranes. That would come later.

I soon met and became acquainted with another young plant physiologist at UC Davis, Joe Key, who was doing a post-doctoral stint in the Biochemistry

Department. We became great friends, and to this day we talk at least every week, vacation together with our families, and genuinely like each other. When I told him about my interest in the biochemistry of ion transport, he said, "You should do a postdoc with my old PhD supervisor, John Hanson, who is at the University of Illinois." So I wrote to Hanson and told him of my interest in investigating the energetics of ion transport across cell membranes, and he invited me to join his group.

Upon arriving at Jack Hanson's lab, I embarked on a project to investigate the energetics of  $\text{Ca}^{++}$  transport into corn mitochondria. My approach was to optimize oxidative phosphorylation, assuming the ATP generated would drive Calcium-45 into the mitochondria. After a few months of failures to achieve significant  $\text{Ca}^{++}$  transport into corn mitochondria, I read a paper by a professor from Ohio State University, George Brierley, in which he was able to demonstrate  $\text{Ca}^{++}$  uptake into beef heart mitochondria. The trick was to omit ADP from the reaction medium so as to minimize ATP production. ATP production and  $\text{Ca}^{++}$  transport were competitive reactions! The next day, at about 5 p.m., I stood in front of the Geiger-Mueller counter as it cycled through the planchets counting  $^{45}\text{Ca}$ , and I nearly wet my pants when it counted the samples from the minus-ADP treatment! The lights on the counter were glowing in continuous streams. It was around this time that Peter Mitchell put forward his chemiosmotic

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hypothesis that a proton/electrical gradient was the driving force for ATP formation and for active ion transport. Mitchell won the Nobel Prize in 1978 for his chemiosmotic hypothesis.

In 1963, the University of Illinois offered me an assistant professor position, and I immediately embarked on a project to determine whether ATP could drive ion transport across the plasma membrane. This led to the finding that, in crude membrane fractions, monovalent alkali cations could activate ATPase(s). In 1971, I moved from the University of Illinois to the Botany and Plant Pathology Department at Purdue University, where I, along with my postdoc Robert Leonard, was then able to eventually show that a  $K^+$ -stimulated ATPase was present on plasma membranes. This in turn led to my graduate student Heven Sze's eventually showing that plants had two distinct  $H^+$  pumping ATPases: one on the plasma membrane and another on endomembranes, including the tonoplast. Both ATPases can generate a pH and electrical gradient across membrane vesicles. Furthermore, the proton electrochemical gradient also could drive other ion and metabolite transport. In 1975, ASPP awarded me the Charles Albert Shull Award for discovering the plasma membrane ATPase, which is now recognized as the "master powerhouse" for transport in all plants.

From 1977 to 1982, I served as head of the Botany and Plant Pathology Department at Purdue University. I enjoyed that role very much; however, I had little time for

research, which was my first love. So I decided to quit being an administrator and go back to research.

In January 1982, I attended the Miami Winter Symposium, and the meeting completely changed my research direction. The first reports of the production of transgenic plants were presented. I was immediately hooked on this science and embarked on a totally new research endeavor—developing methods for regenerating fertile plants from protoplasts of important monocot plants (corn and rice). We (I and Lisa Lee, Jianying Peng, and Halina Kononowicz) were able, for the first time, to successfully produce fertile indica rice plants from protoplasts. We were then able to genetically transform the protoplasts using either polyethylene glycol or electroporation and to regenerate fertile transgenic indica rice plants.

We then embarked on a project to develop a system for producing hybrid rice. My PhD student Jang-Yong Lee was able to isolate from rice a tapetum-specific promoter (RTS), which was then used to drive the barnase gene (an RNase), which prevented pollen development, making plants male sterile. Simultaneously, another postdoc, Leszek Lyznik, was introducing the fungal site-specific recombinase FLP/FRT into corn, rice, and Arabidopsis plants. Under the correct conditions, the FLP gene/enzyme could excise, from the genome, a previously inserted fragment of DNA that was flanked by the FRT sites. Another postdoc, Hong Luo, using rice and bentgrass plants, produced transgenic plants containing the RTS promoter driv-

ing barnase (making male sterile plants) that was flanked by FRT sites. When these plants were crossed with plants containing the FLP gene, the barnase gene was excised and fertility was restored in the progenies. Thus, a new method for making hybrids was developed.

Recall that early on I wanted to be a golf course superintendent and take care of (mow!) bentgrass greens. I didn't get back to turf grasses until the end of my career. One of my last scientific papers was on the production of male-sterile (using the RTS promoter to drive barnase), herbicide-tolerant bentgrass. The male sterility prevents the transfer of foreign genes to other plants, which, in my opinion, should be a requirement for all commercial plant GMOs.

### What do you consider to be your most important contributions to plant science?

Without question, my most important contribution has been the training of graduate students and postdocs who have gone on to make their own contributions. Nearly all of them are still in science or have retired from science!

In research, with the help of these students and postdocs, I think my primary contribution was the initiation of the study of the energetics of ion transport across plant cell membranes—mitochondria and the plasma membrane—and demonstration that ATP was the primary energy source for ion transport. The second most important contribution of my research would be the first transformation

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and regeneration of protoplasts into fertile plants in indica rice, which is arguably the most important food crop in the world. The third most important success was the development of a new system for making hybrid plants, which is also important as it allows for keeping a “gene of interest” (e.g., a gene for producing a specialty chemical) silent while building up a large supply of seeds and then, through crossing, excising a fragment of DNA that allows for expression of the gene of interest in the next generation. This could have significant practical value.

### When did you become a member of ASPP/ASPB?

I became a member of ASPP when I was in graduate school. My first ASPP meeting was in 1960 (I think) at Purdue University. I went to the meeting with my mentor, Yoash Vaadia. Since I grew up on a farm in southern Indiana, I took him to visit the farm and meet my parents. My Israeli mentor was “enlightened” to see what life was like on a family farm, and he seemed to enjoy meeting my parents. My parents, who went only to the eighth and ninth grades, were overwhelmed by this Jewish genius, and they fell in love with him!

### How did the Society impact your career, and what motivated you to become a Founding Member of the Legacy Society?

ASPP/ASPB supported journals that were a good place to publish. Meetings were fun and a great place to meet and interact with other scientists and to learn about the most recent discoveries in our field.

Being involved in the functioning of ASPP/ASPB has also been rewarding. I served on numerous committees during my career. One of the more satisfying committee assignments was as chair of the Long-Range Planning Committee the year *The Plant Cell* was established. As chair, it was my responsibility and challenge to present this proposal to the Executive Committee for approval. I presented it to the Executive Committee in the most positive light possible, but there was substantial opposition, as the new journal was viewed by some as a competitor to *Plant Physiology*. President Charles Arntzen allowed some discussion but, wisely, kept it reasonably short, and the proposal passed and *The Plant Cell* was initiated. Subsequently I was the recipient of substantial blowback from some members of the Executive Committee, but establishing *The Plant Cell* was a significant achievement for ASPP/ASPB, and I

was happy to have been involved in a small way.

My motivation for becoming a Founding Member of the Legacy Society was that I believe that ASPB is the most important plant society in the world, and it must never be allowed to disappear. It needs money to grow and prosper, and I encourage others to join as soon as possible.

### What important advice would you give to individuals at the start of their career in plant science?

Take time to think broadly. Don't be afraid to try new things and to tackle big problems. When you read or encounter something you don't understand, don't pass it over with “I'll try to figure that out later.” Pursue it now—don't procrastinate. Thank your mentors, and take the time to become friends with your students, postdocs, technicians, visiting professors, dishwashers, and undergraduate students. Whatever success I may have had, it was because of these wonderful colleagues.

### Academic Family Tree

<https://academictree.org/plantbio/tree.php?pid=734547>