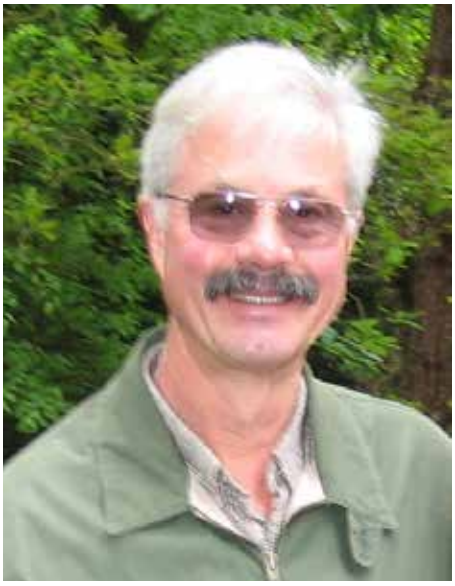
Lincoln Taiz



How did you spend your career?

A scientific career typically begins in graduate school, when one earns a first paycheck as a teaching or research assistant. Mine began in the summer of 1967, when I joined the Botany Department at the University of California, Berkeley, as a PhD student, having arrived by a somewhat unorthodox route. I had dropped out of college during my sophomore year at the University of Pennsylvania and worked for a while at a knitting mill in Philadelphia's garment district (now defunct) with the object of making enough money to travel abroad. As a lapsed English major, I nurtured fantasies of going to Paris to write. But when the time came, the siren call of Berkeley in the 1960s had become irresistible, so I packed a few things and hitchhiked out west. To condense what could fill a novel down to a haiku, I met my future wife, Lee, in Berkeley, and after our wedding we took a Greyhound bus to Salt Lake City, where Lee had a teaching job, and I completed my undergraduate degree in botany at the University of Utah. My conversion from English to botany was partly inspired by Lee, whose lifelong love of plants rubbed off on me during our many hikes through the Wasatch Mountains behind the campus.

The decision to return to Berkeley for graduate school was both personal and professional. Berkeley in the 1960s was a charismatic place, and Lee and I still had many friends there. A stroll through Sproul Plaza was like wandering through the set of a Fellini movie, with a few scenes from *Battleship Potemkin* thrown in for good measure. Scientifically, Berkeley was then the top-ranked botany department in the country, so I was pretty excited after receiving a call from the department chair, Leonard Machlis—the author of the reigning plant physiology lab manual—telling me that I had been accepted to the graduate program.

Upon reporting for duty at the department in the late summer of 1967, I was immediately thrown into the deep end by being assigned as teaching assistant (TA) of an electron microscopy (EM) course that fall. My smug satisfaction at being a Berkeley graduate student abruptly pivoted to panic, for I had little more than a passing acquaintance with the most basic compound microscopes, let alone an electron microscope the size of a Volkswagen bug. Youthful resilience prevailed despite my trepidations, and after a crash course given to me by a kindly EM technician, I was good to go. As far as the students were concerned, I was an expert, and my worst nightmare of blowing up the hissing, clanking, buzzing contraption never materialized. In fact, after my baptism by fire, all subsequent TA assignments seemed like cakewalks by comparison.

In my second year, I joined the laboratory of Russell Jones, then a brash young assistant professor who had recently completed a postdoc with Anton Lang and Joe Varner at the celebrated Atomic Energy Commission (now DOE) Plant Research Laboratory at Michigan State University (MSU). Russell was regarded as something of a prodigy in the department, and I relished the opportunity to work with someone who, like me, was interested in plant hormones, which at the time were pretty much a black box. An expert on gibberellins, he had brought the barley aleurone/α-amylase system with him to Berkeley from MSU. I chose as my research project the mechanism of gibberellic acid (GA)–induced cell wall degradation in barley aleurone layers, a spinoff of Russell's elegant electron microscope studies. In the process of characterizing the synthesis and secretion of various GA-induced hydrolases presumed to be involved in cell wall degradation, I developed a method for isolating aleurone cell protoplasts that were capable of undergoing cellular autolysis in vitro. Serendipitously, in the process of isolating protoplasts I discovered a novel enzyme-resistant inner wall layer that encased each plasmo-

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desma like an exoskeleton. To my knowledge, this curious observation has never been followed up.

After my PhD, I stayed on in the Botany Department an additional year as an NSF postdoctoral fellow, followed by a year as an acting assistant professor. I was then lucky enough to be hired by the Biology Department at UC Santa Cruz, one of the most beautiful campuses in the world, where I progressed through the professorial ranks until my retirement in 2007. From cell wall degradation in aleurone layers, my thoughts turned to the question of how cell walls regulate cell expansion during stem and coleoptile elongation. Progress had previously been made along two fronts: Bob Cleland's studies on the role of cell wall acidification in causing auxin-induced growth in coleoptiles, and Paul Green's biophysical analyses of cell expansion using the giant algal cells of *Nitella* as a model system. I wondered whether cell wall acidification might also be involved in the mechanism of cell elongation in *Nitella* internode cells. Taking advantage of the naturally occurring acid and alkaline bands along *Nitella* internode cells, Jean-Pierre Metraux, a new Swiss graduate student in my lab, was able to show that proton extrusion did indeed regulate the growth rate of *Nitella* cells. He also performed a series of elegant in vitro experiments on isolated *Nitella* cell walls characterizing the effects of pH on wall mechanical properties under multiaxial stress conditions that mimicked turgor pressure.

Hoping to drill down a little closer to the core mystery of auxin-induced cell elongation, my attention next focused on the enzyme responsible for proton pumping—the plasma membrane (PM) H^+-ATPase. With Mark Jacobs, who spent a sabbatical in my lab in 1979, I showed that vanadate, a PM ATPase inhibitor, blocked auxin-induced proton extrusion and elongation in coleoptiles and pea epicotyls. The next step was to develop a membrane vesicle system that would allow us to study the regulation of the vanadate-sensitive proton pump in vitro. Fortunately, Irv Mettler, fresh from a postdoc in Harry Beevers's lab, joined my lab at this time. Irv was experienced at isolating membrane fractions on sucrose gradients, and he and Suzanne Mandala, a recently arrived graduate student from Swarthmore, set about isolating proton-pumping PM vesicles from corn coleoptiles using a fluorescence quenching assay.

They soon identified a membrane fraction that exhibited strong activity. The problem was that the activity was in a lighter fraction at the top of the gradient rather than midgradient where the PM marker enzymes were concentrated. Irv had a hunch the proton pumping activity was actually localized on the vacuolar membrane rather than the PM, and he turned out to be right. Although we were initially disappointed, the vacuolar proton pump had not yet been characterized, and as it turned out, other labs were converging on the same discovery. Fortuitously, our lab neighbors, Barry and Rusty Bowman, had identified a similar fraction in *Neurospora,* and Heven Sze and others were arriving at the same conclusion for plants. Within a year there emerged an entire constellation of labs investigating the vacuolar H^+-ATPases of animals, plants, and fungi, with the plant and fungal labs leading the way.

During the latter phase of my research career, my focus shifted to other related topics, including hyperacidification in lemon fruits, heavy metal tolerance, and auxin transport—work spearheaded by postdoc Mathias Müller from Switzerland and graduate student Angus Murphy.

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

By the late 1980s, molecular biology was in full swing, and techniques for cloning and sequencing genes had become essential laboratory tools. For me it was a challenging transition from physiology to molecular biology, just as earlier it had been difficult for plant anatomists to adapt to the electron microscope. I was very fortunate in having a lab full of extremely talented postdocs and graduate students at this crucial moment. To facilitate communication and create a sense of esprit de corps, the Taiz and Bowman groups began holding joint lab meetings, and some of my fondest memories are from this period. Suzanne Mandala had succeeded in purifying the V-ATPase of maize and identifying various subunits on electrophoretic gels. In parallel, Rusty Bowman had identified the same subunits in the *Neurospora* V-ATPase. The creation

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of antibodies enabled us to localize the protein on the plant vacuolar membrane by EM immunocytochemistry. More importantly, we able to clone two of the genes from a carrot cDNA library using the maize antibodies, and the Bowman lab cloned the same genes in *Neurospora*.

The sequences of the A and B genes turned out to be homologous to the β (catalytic) and α (noncatalytic) subunits, respectively, of the F-ATPases of eubacteria, chloroplasts, and mitochondria. In addition, our scanning EM examination of the intact structures of the V- and F-ATPases of both carrot and *Neursopora* revealed "ball and stalk" structures similar to those of the F-ATPases. However, the catalytic A subunit of V-ATPases was larger than the F-ATPase β-subunit, and Henrik Kibak, a graduate student in my lab, wondered why. He therefore divided the A subunit sequence into six sections and searched for homologs of each. He discovered that all of the fragments were homologous to the β subunit of F-ATPase except the second one located just upstream of the catalytic site. He dubbed this sequence the "nonhomologous region." Because it seemed to be remotely related to some virus sequences, we speculated that it represented an ancient insertion event.

The next phase of the V-ATPase story revealed the evolutionary relationship of the V-ATPases of eukaryotes to the A-ATPases of archaebacteria, which set the stage for rooting the phylogenetic tree of life. The breakthrough came with the sequencing of the ATPase operon of the archaebacterium *Sulfolobus acidocaldarius* by Masasuke Yoshida's lab in Japan. In 1989, Yoshida presented his results at the Bioenergetics Conference at the University of Osnabrück in Germany. During his talk, he showed an overhead of the amino acid sequence of the *Sulfolobus* catalytic subunit. From my perch in the upper seats of the lecture hall, I quickly scanned the sequence to see whether it contained the nonhomologous region, which would indicate that it was closely related to the eukaryotic V-ATPase. And it was there, just where it was supposed to be, immediately upstream of the catalytic site! It was an electrifying moment. The eukaryotic V-ATPase, or at least its catalytic subunit, was clearly more closely related to the archaebacterial ATPase than it was to the eubacterial F-ATPase. As we broke for lunch, I literally ran down Masasuke in the hall to tell him the news. We quickly inserted the carrot V-ATPase catalytic subunit sequence above the *Sulfolobus* sequence of his overhead, and when the session resumed Masasuke was given special dispensation to present it to the astonished audience. Subsequently we determined that the amino acid sequences of the eukaryotic A and B subunits were about 50% identical to the β and α subunits of *Sulfolobus* and only 25% identical to those of eubacteria F-ATPases.

Peter Gogarten, a postdoc from Germany, had been working closely with Henrik Kibak on the evolutionary relationships of the V- and F-type ATPases. It was clear that the catalytic and noncatalytic subunits were paralogous, having arisen from a gene duplication event as in the case of the β and α subunits of eubacteria. By constructing a united phylogenetic tree that included both the catalytic and noncatalytic subunit genes, Peter was able to infer that the gene duplication event must have occurred prior to the last common ancestor of the eubacteria, eukaryotes, and archaebacteria. This allowed him to place the root of the phylogenetic tree of life between the eubacteria on the one hand, and the eukaryotes and archaebacteria on the other. It further suggested that eukaryotic vacuolar ATPases had evolved from internalized archaebacterial ancestral genes. How this internalization occurred remains an ongoing question.

Finally, beginning in the late 1980s, I began a 30-year collaboration with Eduardo Zeiger on an upper division textbook *Plant Physiology*. The idea behind the book was to follow the example of James Watson's classic text *Molecular Biology of the Gene,* which used declarative sentences as heads for the various subsections. These sentence headings were intended to summarize the take-home message of each subsection—articulating, in effect, the salient principles of plant physiology. From a practical standpoint, the use of multiple authors enabled us to carry on our own research programs while periodically producing new editions of the book. Now titled *Plant Physiology and Development,* the text is in its sixth edition and includes two more

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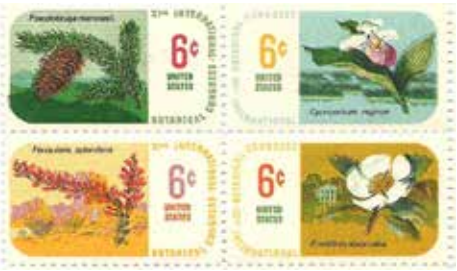
editors, Angus Murphy and Ian Max Müller. We recently produced a shorter version titled *Fundamentals of Plant Physiology*.

When did you become a member of ASPP/ASPB?

I believe it was the summer of 1969, when I attended the XI International Botanical Congress (IBC) in Seattle as a graduate student. That year, the ASPP annual meeting was held jointly with the IBC. The IBC was a major event for Seattle and was welcomed with much fanfare. The United States Postal Service even issued four new 6-cent stamps for the occasion.



Three of my fellow grad students and I had driven there not only to soak up as much information as possible, but also to engage in a bit of political agitation, for which Berkeley students were notorious. The Presidential Symposium was slated to highlight research by plant biologists aimed at increasing agricultural yields to feed a rapidly expanding population. Inspired by Paul and Anne Ehrlich's *The Population Bomb,* which had been published the previous year, our goal was to persuade members of the IBC to pass a resolution to the effect that, despite the best efforts of plant biologists to increase the food supply, it would be impossible to feed an ever-expanding population without some limits on population growth. To this end we had crafted a petition with the intention of setting up tables in the conference hall, hoping to gain enough signatures to sway the IBC to adopt our resolution.

After registering and settling into our dorm rooms at the University of Washington, we set up two tables in the lobby of the student union and took our seats behind them. It wasn't long before curious delegates began stopping by to read the petition. To our relief, the majority of those stopping by signed the petition! Over the next few days, delegates from every country signed on, except those from Canada and the Soviet Union (the latter accompanied by their "minders"), who declined to sign on the grounds that their countries needed more people to achieve their economic goals.

When the *Seattle Times* published a story about us a couple of days into the meeting, the conference organizers began to worry that our petition was undermining the primary purpose of the Presidential Symposium, which was to highlight the contributions plant biology was making toward feeding a growing population. The next day the organizers contacted us to arrange an urgent meeting with the president. We were giddy with excitement. The president was none other than the legendary plant physiologist Kenneth V. Thimann, who was to become my dear colleague at UC Santa Cruz four years later. As we took our seats at the large rectangular table with Kenneth at the head, we prepared to lock horns with this gray eminence and hold our ground at all costs. Whatever was actually going on in his mind, Kenneth proved to be a polite, soft-spoken, and completely disarming adversary, and after we had made our case, he readily agreed to put our resolution to a vote at the plenary session of the Congress. True to his word, the vote was taken, and the resolution passed with flying colors. The next day our small but happy band of graduate students drove home to Berkeley in triumph, certain in the knowledge that we had struck a blow for a sustainable future in which everyone had enough to eat.

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

One of the attractions of a scientific career to me has always been the collaborative nature of research. Experimental scientists are nothing if not social, and even theoreticians depend on regular feedback from their colleagues. For those of us working in plant biology, ASPB provides a formal structure that facilitates easy communication among its members, whether through its journals, annual meetings, sectional meetings, or website. For graduate students and postdocs, ASPB provides access to job opportunities, future mentors, and legendary figures in the field. In essence, ASPB is our tribe, fostering communication, collegiality, productivity, and visibility at every stage in our careers. The officers of ASPB also play a vital role as ambassadors and lobbyists for continued

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government funding for research and education, which impacts us all. Becoming a member of the Legacy Society was simply my way of expressing appreciation to ASPB for all of the important work it does.

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

Time management will be one of your greatest challenges right off the bat, unless you are one of those fortunate individuals to whom it seems to come naturally. Besides writing grants and setting up a lab, you will probably have teaching and administrative duties to fulfill as well. Being able to multitask and deal with stress is foundational to everything else. Self-doubt is natural, but you should feel confident that you belong where you have arrived. After all, most jobs are extremely competitive, and you have already been thoroughly vetted by your new colleagues.

Work on establishing rapport with the people around you, especially the students in your lab. Undergrads need a lot of direction. Graduate students and postdocs differ in their needs, depending on their skills and independence, so you need to tailor your approach to each individual. By the time they leave your lab, however, postdocs should be functioning as independent investigators.

As far as research topics are concerned, I suggest letting your curiosity be your guide, with a couple of caveats. First, don't let competition from other labs deter you from pursuing a question that interests you. The sexiest problems tend to be the most competitive. Second, be opportunistic. If a novel and exciting result lands in your lap, don't put it aside it because it wasn't what you originally set out to investigate. Finally, as my experience at the 1969 Seattle International Botanical Congress shows, even graduate students can influence public policy issues within scientific societies if they make their voices heard.

Academic Family Tree
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