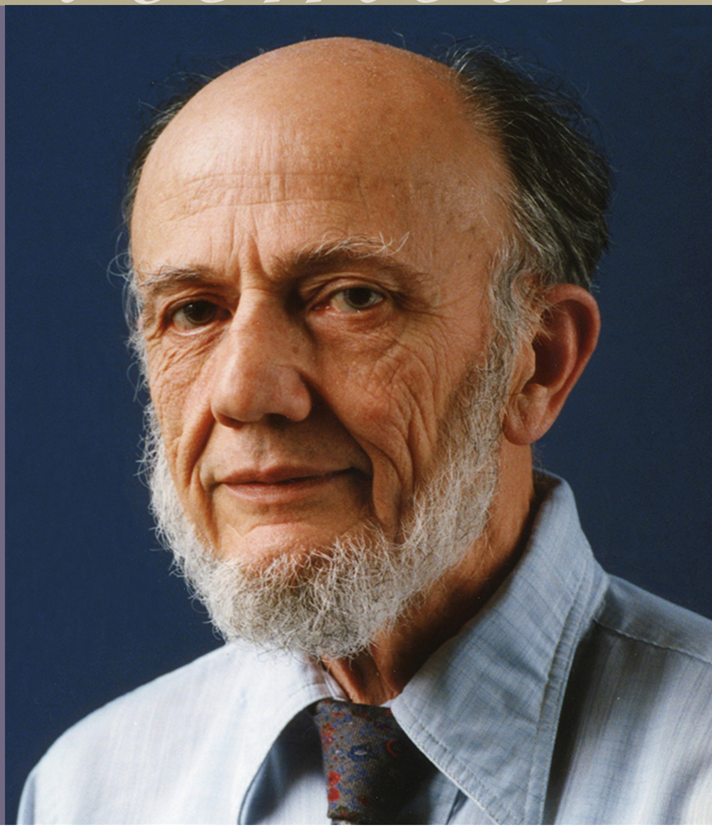
André T. Jagendorf

1926–2017

BIOGRAPHICAL *Memoirs*



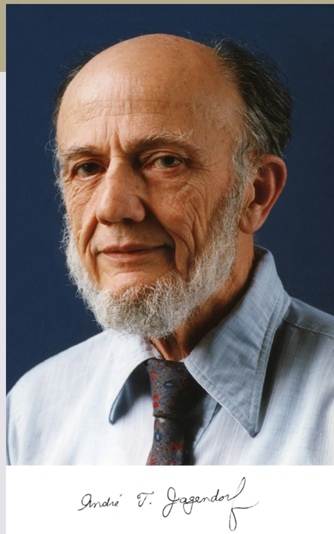
A Biographical Memoir by
Richard (Dick) E. McCarty
and Devaki Bhaya

NATIONAL ACADEMY OF SCIENCES

ANDRÉ TRIDON **JAGENDORF**

October 21, 1926–March 13, 2017

Elected to the NAS, 1980



Photography by Craig Cramer, Cornell University.

By Richard (Dick) E. McCarty and Devaki Bhaya

André Tridon Jagendorf had a long and distinguished career in plant biology, but he is best known for his seminal discoveries in the field of photosynthesis. His elegant and carefully planned experiments provided the first strong evidence in support of Peter Mitchell's chemiosmotic hypothesis. Mitchell had proposed that the electrochemical proton gradients generated across the membranes of mitochondria or chloroplasts by electron transport could power the synthesis of adenosine 5´- triphosphate (ATP). This hypothesis was largely scorned by Mitchell's colleagues, especially since there was no experimental evidence available. Jagendorf's seminal contribution was to provide the first strong evidence, using membranes from chloroplasts, in support of this controversial idea. Jagendorf continued to carry out novel experiments that deepened our understanding of how ATP formation is linked to the capture of light energy in a process called photophosphorylation. What is now acknowledged as fact in textbooks on biochemistry or on photosynthesis, was based on the series of experiments carried out by his group.

Jagendorf earned a B.S. degree in plant physiology from Cornell University in 1948 and a Ph.D. in biophysics from Yale in 1951. He also did post-doctoral work at UCLA from 1951 to 1953. While there, although a botanist, he was offered a faculty position in the Johns Hopkins University Department of Biology, where he remained until 1966. He moved to Cornell as a professor of plant physiology that year, becoming, on his retirement in 1997, Cornell's Liberty Hyde Bailey Professor Emeritus.

André Jagendorf was born on October 21, 1926, in New York City. His Austrian-born father, Moritz A. Jagendorf, entered Yale Law School, but transferred to Columbia University to be "near the theater." He practiced dentistry in Manhattan part-time for 40 years. He was a theater agent and director, a producer, playwright, puppeteer, and, later, a prolific writer of folk stories for children based on American and European folk tales.

André's mother, Sophia Sokolsky Jagendorf, was a teacher but began her career as an innovator in modern dance. She worked with her husband on several books on folklore.

One can easily imagine that the Jagendorf household provided André a stimulating intellectual environment. Many of Moritz's patients were artists, and it is likely that André was exposed to some of their work. André attended the Bronx High School of Science (Class of 1944). It was then (and still is) very hard to gain admission. He modestly claimed that his decision to apply was motivated by his reading of science fiction books. Among his schoolmates were Bruce Ames, Charles Yanofsky, and Norton Zinder, all of whom went on to very distinguished careers in the biological sciences.

Undergraduate Years

One might wonder what attracted a young man who was raised in New York City to study plants. André related that his father found farmland vistas appealing and suggested that André study agriculture and become a farmer. The fact that, at the time, New York State residents could attend the College of Agriculture at Cornell University tuition free may also have been a factor. Although André was an avid gardener, he wasn't cut out to be a farmer, finding the sciences more appealing. He was admitted to Cornell, where he majored in botany. One of his first courses was "Vegetable Crop Production and Marketing." He claimed that he scored 100 percent on the final exam of the course. He took courses in plant physiology that excited him. But it was working in a lab during the summers on plant-related research that convinced him that a career in the plant sciences was his destiny.

In an interview with Bob Turgeon in 2016, André revealed that he had voluntarily enlisted in the Army Air Force during his sophomore year at Cornell. He went through basic training in Texas and was being trained in photography when he hurt his foot and ended up in the infirmary. The war was over, but his unit was deployed as a part of the occupation force in Germany.

Graduate Years

André graduated from Cornell with a bachelors' degree in botany and joined Yale's newly formed Department of Botany and Microbiology in quest of a doctorate. He wanted to work in the lab of Paul R. Burkholder, the chair of the department. Burkholder was a botanist who had switched his research focus to the study of fungi and discovered the compound chloramphenicol, now widely used as an antibiotic. However, André was assigned, instead, to the lab of David Bonner, an assistant professor with an interest in leaf growth factors. Bonner had been a postdoctoral associate of Edward Tatum and George Beadle at Stanford and came to Yale in 1945 along with Tatum.

By 1948 Bonner's research interest had shifted completely from plants to the fungus *Neurospora*, and André was Bonner's last graduate student to work on plants. André's thesis research was guided by Aubrey Naylor, an assistant professor who subsequently had a long and productive faculty career at Duke University, researching plant biochemistry and physiology. André studied the effects of the herbicide 2,4-D on the growth of the roots of cabbage seedlings. He found that 2,4-D induced abnormal growth of the roots that resembled tumors. Four journal articles based on his thesis research were published, an accomplishment that is made even more remarkable by the fact that André received his Ph.D. in three and one-half years!

While he was still a graduate student at Yale, André spent part of a summer working in a plant biology lab in southern California. There, he met Sam Wildman, a UCLA faculty member and a former postdoctoral associate of James F. Bonner at Caltech. David and James Bonner were brothers. James Bonner and Sam Wildman carried out ground-breaking experiments that led to the isolation of organelles and soluble proteins from cells. André was anxious to work with Wildman and he got his chance when he was awarded a prestigious Merck Postdoctoral Fellowship in 1951.

André called his two years at UCLA "the happiest of his life." Using differential centrifugation and filtration of cell-free homogenates of tobacco leaves, he prepared fractions that were enriched in chloroplasts and showed that they were not contaminated by mitochondria. This work was described in a paper in *Plant Physiology* and in an article in the *Annual Reviews of Plant Physiology.*

Faculty Years

While at UCLA, André received a phone call from William D. McElroy, Director of the McCollum-Pratt Institute and faculty member in the Biology Department at Johns Hopkins University in Baltimore. McElroy, a biochemist, was very well known for his work on firefly luminescence and later became head of the National Science Foundation and chancellor of the University of California, San Diego. At the time, McElroy was actively recruiting faculty to the Institute and the department and André was on his list, since McElroy was a friend of David Bonner. Sight unseen, he offered André a faculty position. André asked if he could visit Hopkins, but McElroy said a visit wasn't necessary and that André could simply show up in the fall of 1953. André accepted the offer, even though he thought that he would be the "token botanist" in the Biology Department at Hopkins.

André had never had a course in biochemistry, yet most of his younger colleagues at Hopkins were biochemists or biophysicists. Fortunately, there were frequent seminars, journal clubs, and major symposia (*Light and Life*, for example), and André was a fast learner. He also interacted closely with his new colleagues, including Ludwig Brand, Maurice Bessman, Anthony San Pietro, Sigmund Suskind (also a graduate student of David Bonner) and Philip Hartman. The 1950s and the 1960s were an exciting period at Hopkins as it pioneered the fields of cell biology, biochemistry, molecular and developmental biology.

In 1953, when André started at Johns Hopkins, the complexity of photosynthetic processes was still being revealed. James Bassham, Andrew Benson, and Melvin Calvin at UC Berkeley had elucidated the pathway of carbon dioxide reduction (the so-called "dark reactions") of photosynthesis in 1950. Much less was understood about the "light reactions" (electron transport and ATP formation), although it was clear that both a strong reducing agent and ATP were required to power photosynthesis. In 1954, Daniel I. Arnon, F. R. Whatley, and Mary Bell Allen reported that illuminated chloroplast membranes can carry out photophosphorylation, the light-dependent synthesis of ATP from ADP and inorganic phosphate (Pi). The major question was whether there was a "high-energy" intermediate that coupled electron transport to ATP synthesis.

André devised an innovative experimental protocol to test this idea by separating photophosphorylation into two stages: light and dark. He illuminated chloroplast membranes under conditions in which they carried out electron transport and then injected the mixture into a solution that contained ADP and Pi, in the dark. Significant amounts of ATP were formed, suggesting that an intermediate created in the light could drive ATP synthesis in the dark. He called this intermediate "X_E,"—X for unknown intermediate and "E" for energetic—and conjectured that X_E was likely to be a proton concentration gradient, at the time an untested and unusual concept. His group also made a most astounding discovery: that proton gradients generated artificially across chloroplast membranes in the dark could drive ATP synthesis. These landmark experiments were truly paradigm-shifting and established that light-dependent electron flow generated an electrochemical proton gradient across a membrane, which in turn could lead to the formation of ATP. André was soon promoted to full professor with tenure at Hopkins.

André continued his quest to purify chloroplasts via density gradient centrifugation. In fact, this proved challenging, and instead he succeeded in getting purified preparations of thylakoid membranes, which were densely packed inside chloroplasts. Importantly, these membranes were robust and retained many of their activities after isolation. It is worth noting that intact chloroplasts were not isolated in high yield until many years later. André and Sam Wildman found very little nucleic acid in their “chloroplast” preparations, because they did not contain intact chloroplasts and the assays for detection of nucleic acids were not very sensitive. They concluded that “chloroplasts have no nucleic acid.” Years later. in his short memoir, André characteristically noted this error with a terse sentence “Dim excuses!” This reflects a typical response, where André would go after a big question and often succeed, but always note with humility and humor where things went wrong.

The biochemists at Hopkins were interested in the structure and function of biological systems. McElroy and Mordhay Avron, André’s postdoctoral associate, convinced André to begin studying what the chloroplast preparations could do. Since the late 1930s it was known that thylakoid membranes can reduce added oxidizing agents and evolve oxygen in the light. The oxygen is formed by the oxidation of water. This was known as the “Hill Reaction.” During the mid-1950s André and his colleagues David Krogmann, Mordhay Avron, Maurice Margulies, and Georgio Forti and lab technicians Marjorie Evans and Marie Smith carried out a remarkable series of experiments, first on chloroplast electron transport and, a bit later, on the coupling of ATP synthesis to electron transport. Avron was especially productive. In some of the research, André’s lab was in direct competition with that of Daniel I. Arnon, the discoverer of photophosphorylation and a well-respected senior plant physiologist. André more than held his own and demonstrated, without a doubt, that ATP synthesis by thylakoids was coupled to light-dependent electron transport.

André and Avron also discovered the chloroplast enzyme they called “TPNH Diaphorase.” TPNH was an older abbreviation for reduced nicotinamide adenine dinucleotide phosphate (NADPH). The enzyme catalyzes the reduction of a number of compounds, including dyes, by NADPH. Now, André was a practicing enzymologist! This enzyme, a flavoprotein, is now known to be part of the chloroplast electron transport chain, where it functions to generate NADPH to be used in the reduction of carbon dioxide to sugars.

Although André may have been the only botanist at Hopkins, he was not the only biology faculty member working with plants. Tony San Pietro studied another component of the chloroplast electron transport chain that was required for thylakoids to reduce $NADP^{+}$. Tony called this component “Photosynthetic Pyridine Nucleotide Reductase” (PPNR). PPNR, later known as ferredoxin, reduces the flavoprotein, which in turn reduces $NADP^{+}$ during light-dependent electron transport in thylakoid membranes.

Geoffrey Hind, a postdoctoral associate from England, and André thoroughly characterized both the light and dark stages of “two stage” ATP synthesis. There was no doubt that the same intermediate drove ATP synthesis in thylakoids both under continuous illumination and in the dark after illumination. The ATP yields in the two stage assays far exceeded the content of the components of the electron transport chain. This observation was puzzling, as it was inconsistent with the prevailing hypothesis of how ATP synthesis and electron transport are linked.

In their characterization of two-stage phosphorylation, Geoff and André investigated the dependence of both the light and dark stages on pH. Their experiments were impeccably controlled. They ran controls in which thylakoids were incubated at various pH values in the dark prior to their injection into ADP and Pi at pH 8.0, the optimum pH for ATP synthesis. They found that some ATP was made when thylakoids were incubated at pH 4 in the dark and then injected into a mixture that contained ADP and Pi at pH 8. They were very cautious in their interpretation of this result, suggesting that pH gradients that were generated artificially in the dark may drive ATP synthesis by thylakoids, but that was just one possible interpretation.

Just a year later, André and Ernest Uribe, another postdoctoral associate, showed that very high amounts of ATP could be made entirely in the dark if certain buffers were present in the acid stage. The amount of ATP formed depended on the pH difference between the acid and base stages and was affected by reagents that inhibited photophosphorylation. They concluded that their results were consistent with Mitchell’s chemiosmotic hypothesis. André’s lab had produced the first dramatic evidence in favor of the hypothesis, a remarkable achievement that justly received worldwide recognition.

André, Geoff, and Joseph Neumann also showed that light-dependent electron transport resulted in an accumulation of protons in the thylakoid internal space. They could monitor this process simply by measuring the pH of thylakoid suspensions. This light-induced pH rise reversed in the dark and was sensitive to uncouplers of photophosphorylation. Taken together, these results strongly indicated that X_E is the proton gradient generated in the light by electron transport.

Several aspects of chloroplast molecular biology and development always piqued André's interest. John Mego showed that in the primary leaves of dark-grown bean plants, plastid growth was stimulated by red light but could be reversed by far-red light. This suggested that phytochrome was the photoreceptor. Alva App worked on aspects of chloroplast development in *Euglena* as well as protein synthesis by isolated chloroplasts. André was very excited by the latter project, but it was found that most of the amino acid incorporation was by bacteria that contaminated the chloroplasts. Not willing to give up readily, M. Bamji and André isolated plastids from young wheat seedlings that incorporated leucine into proteins in a manner that was inconsistent with bacterial contamination.

Around this time Cornell University, André's alma mater, reached out to him, and even though he had recently been promoted to full professor at Hopkins, he found the Cornell offer attractive. He held fond memories of his undergraduate years there, and it is likely that the prospect of having a large number of colleagues in the plant sciences was appealing to him. He joined the Cornell faculty in 1966.

The mid-1960s were an especially exciting period for the biological sciences at Cornell. A Division of Biological Sciences was formed in 1964 and new faculty actively recruited. Efraim Racker moved from New York City to be the Albert Einstein Professor of Biochemistry and guided the hiring of junior and senior biochemists .

André was hired as professor of plant physiology in the newly formed Section of Genetics, Development and Physiology. He was justly famous, and graduate students, visiting scientists, and postdoctoral associates too numerous to mention flocked to his lab. One of us (DB) remembers that his students, now professors at various universities, would visit the lab and exchange stories about the good old days. The Clayton lab was also on the same floor, and conversations with Rod Clayton and his lab members and ours, often held late at night with a few libations, were enriching in so many ways!

André became increasingly interested in the enzyme that makes ATP, the chloroplast ATP synthase (CF1-CFo). Although similar to the ATP synthases of eubacteria and mitochondria, CF1-CFo has unique properties, including regulation of the enzyme's activity. Not much was known about the enzyme at this time but it piqued André's interest, and he was intrigued by the roles of the many subunits of the enzyme and its potential for conformational changes. Although thylakoid membranes can form ATP at high rates during illumination, the rates of the reverse reaction, ATP hydrolysis, in the dark are quite low. André and his coworkers showed that changes in the structure of the enzyme are elicited by the proton gradient formed in the light. As André noted, "I was inspired to think about conformational movements of these subunits by the earlier finding of R. McCarty that one of the free -SH groups of CF 1 is attacked by N-ethylmaleimide only when the thylakoids are illuminated."

An especially dramatic demonstration that CF1 undergoes structural changes during light-dependent electron flow was the finding that the presence of light would enhance proton exchange between groups on the protein and tritiated water in the medium. Another intriguing observation was that illumination of thylakoids in the presence of ADP and sulfate, a Pi analog, caused a partial inhibition of ATP synthesis. André was very inventive and willing to try procedures that others had never thought of, or thought would not work. Those of us who needed to prepare CF1 in large amounts praised him for finding a way to concentrate CF1 in very large volumes of EDTA solutions.

Many of André's post-docs and graduate students at Cornell worked on various aspects of protein synthesis in chloroplasts. They included A. Gnanam, Mahtab Bamji, Linda Gooding, Harry Roy, Kar-Ling Tao, Richard Patterson, Len Fish, Josh Hurewitz, Helen Nivison, Ruth Alscher, Taibo Yamamoto, and Devaki Bhaya. They perfected conditions that resulted in high rates of protein synthesis in chloroplasts and showed that a significant fraction of chloroplast ribosomes are bound, as polysomes, to thylakoid membranes. The alpha and beta subunits of CF1 are encoded by plastid DNA and were shown to be synthesized by these ribosomes bound to thylakoids. Subunit III of CFo, a small hydrophobic protein, was also found to be made by thylakoid-bound polysomes. Light, which promotes chloroplast development, increases the proportion of pea chloroplast ribosomes bound to thylakoids.

It was an exciting time for many of us who were in the lab. In the '80s, plastid molecular biology was a rapidly growing research area, and new tools to dissect chloroplast biogenesis were being developed. In his personal perspective *Chance, luck and photosynthesis research: An inside story*, André wrote, "Eventually, the era of DNA technology caught up with me." This is another example of how André was fearless and took the lab in a new direction when his intuition and interest told him this was an important frontier. His lab put the technology to good use. DNA strand-exchange activity with properties that resemble those of RecA from *E. coli* was shown in extracts. A search of an *Arabidopsis* genomic cDNA library led to the identification of a RecA homolog. A recombinant form of the *Arabidopsis* putative RecA protein was expressed in *E. coli* and shown to have RecA activity. This was the first RecA homolog found in a eukaryote.

Family Life

André's relationship with Jean Elizabeth Whitenack got off to a stormy start–literally. They met on a blind double date in Long Island in November of 1950. A violent hurricane had swept through the area and knocked out power, causing considerable damage. Jean and her friend could not travel to New York as planned. As Jean related, "However, nothing daunted André, so he and his friend decided that they would come to us instead." It was quite a trek they made, but well worth it. The date was the beginning of a happy 67-year relationship. Jean and André married in 1952 and spent a year in California while André was finishing his postdoctoral stint. In the summer of 1953, Jean said "We hiked and camped our way across the US to Baltimore and Johns Hopkins."

The Jagendorfs lived in a Baltimore suburb, and their three children, Suzanne, Judith, and Daniel, were born in Johns Hopkins Hospital. Sadly, Daniel died at age 49. Perhaps taking after his paternal grandfather, Daniel had worked in New York theaters. Jean and André had eight grandchildren and eighteen great-grandchildren. Jean is a master lace maker, and for many years she has been a teacher of lace making and a leading member of the Finger Lakes Lace Guild. Remarkably, she was able to describe André's last lab project in detail years after his death.

Jean and André were very kind to the members of André's lab and hosted lab parties in their home. They even held a lovely wedding celebration for a lowly graduate student (REM) and his bride. After the move to Cornell, the Jagendorfs lived in a beautiful house on Ithaca's West Hill. The house was nextdoor to Ef and Frances Racker's and had a spectacular view of Cayuga Lake. One of us (DB) remembers visits to their home, where many original paintings hung on the walls, and André was always ready to provide additional details of a painting and the painter. André enjoyed playing the viola even later in his life and supported the Cayuga Chamber Orchestra by endowing the orchestra's associate violist's chair.

Guests always felt welcome in Jean's and André's home, and were well taken care of and felt part of the family no matter their status in the lab. Being a foreign graduate student (DB) who had come directly from Calcutta to Cornell, I needed to learn innumerable things culturally and intellectually. André was always willing to teach me the ropes and made no judgments but had noticed I was shy and timid. Indeed, after I spent a few months in his lab, he said with a chuckle, "You seem to be excelling in all your classes, but I suggest you take one more course. I think you need a course on 'aggressiveness training.'" This was decades before questions of how to retain women in STEM became a national discussion, but in his iconoclastic and humorous way, André had hit the nail on the head.

Later Years

On his retirement from Cornell in 1997, André was appointed Liberty Hyde Bailey Professor Emeritus. He gave up his lab and teaching, but not his research. He actively collaborated with Dr. Tetsuko Takabe and others on aspects of abiotic stress in plants. Until shortly before his death André worked in Dr. Robert Turgeon's laboratory at Cornell. His last project involved the control of leaf growth, a subject André had maintained an interest for more than 60 years. Turgeon wrote: "One was on the interesting phenomenon that many dicotyledonous species respond to defoliation by resuming growth of remaining mature leaves. Under the right circumstances these leaves can double in size and double their photosynthetic capacity per unit area. It seems most likely that the stimulant comes from the roots. André obtained xylem sap and was able to show that it does indeed stimulate the growth of isolated leaf discs. He was partially successful in identifying the growth factor(s) and worked on the project until a few days before he died. But the other true contribution he made was working with students and postdocs in the lab. He offered wonderful advice, and he often assisted with their experiments. On many occasions he acted as an unpaid technician, helping undergraduates to complete their projects while they were in class or home for the holidays. We always had lunch as a group, and he had many stories—and jokes—to tell and a great deal of useful advice to impart. A number of foreign students and faculty, several from China, were in the lab over the years and they were, rightly so, in awe.

André's list of honors and awards is, not surprisingly, impressive. He was elected to membership in the National Academy of Sciences in 1980, received the Charles Kettering Award (1978) and the Charles Reid Barnes Life Membership Award (1989) from the American Society of Plant Physiologists (ASPP), and was a member of the Pioneer Legacy Society. He was president of the ASPP in 1967. He received a Lifetime Achievement Award in 2012 from the Foundation for Basic Research.

Parting Thoughts and Anecdotes

André showed none of the arrogance that scientists of his stature often display. Despite all this intensive research, André was extremely conscientious about his other responsibilities as a faculty member. It is not uncommon for elite scientists to shirk their departmental administrative and/or teaching duties, but not André. He was chair of his department at Cornell for six years. He taught plant physiology and plant biochemistry and served on many doctoral committees. He did his fair share or more. Many of his students and postdocs remember his corner office, where André would sit engrossed at work amid bound copies of theses and book-lined shelves. If his door were slightly ajar, we would timidly enter to show him our latest results or propose follow-up experimental plans. His intuition was often correct, and he did not mince words if he thought the plans were not well thought out but was equally enthusiastic about good ideas. He treated everyone with respect, even undergraduate students.

Much has been made of André's jokes. Some were even funny. André simply enjoyed making people laugh. He was also extremely kind. André wanted to be helpful and always was. He even bought the champagne to celebrate someone else's student's (REM's) successful defense of her Ph.D. dissertation. One of us (DB) remembers a gift package that arrived when she let André and Jean know of the arrival of her baby daughter. Among the gifts was a gorgeous pink wool cape with a note that said, "No little girl should be without one." Len Fish, one of André's former students,contributes this story: "Twenty or so years after graduate work in André's lab at Cornell, he and Jean visited us and brought for each of the young triplets an Audubon bird with an authentic song, an event which the 'kids' still remember as a special occasion." Ruth Alscher Grene remembers that "André would listen to only a very few minutes of any weekly Plant Physiology seminar, then he would take a nap, and after the polite applause had died down, he would ask a wondrously perceptive question of the speaker. I asked him how he was able to do that and he told me that he only needed a brief introduction to the seminar topic to see what it was about, and what the results were going to be. To me, that was a magical brilliance that I could only admire, and never hope to emulate. I tried, over many years, as a faculty member, to evoke this example. By me, this is what being a mentor is about. The profession is enhanced and enriched by teachers such as André."

Scores of students, postdoctoral associates and visiting scientists from around the world benefited from being in his lab, and each of us passed on at least some of André's wisdom to our associates. We appreciate the value of excellent teaching skills and genuine mentoring. André would have been happy to note that his landmark experiments are now used to teach students in high school and college about classic experiments in biology and the scientific method. We remember with fondness and respect how much André embodied the true spirit of scientific discovery and his non-conformist attitude. He lives on in each of us.

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