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ANTON LANG

1913—1996

A Biographical Memoir by HANS KENDE AND JAN A.D. ZEEVAART

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Biographical Memoir

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Anton Lang

January 18, 1913–June 24, 1996

BY HANS KENDE AND JAN A. D. ZEEVAART

A NTON LANG DIED on June 24, 1996, in Oxford, Ohio. He belonged to a group of eminent plant physiologists who had a profound influence on the field through their research, writings, and public service. Anton's scientific interest focused on plant development, particularly on photoperiodic regulation of flowering. His writings, especially the scientific reviews, set a standard that is hard to match. His dedicated public service culminated in chairing a committee of the National Academy of Sciences that was appointed to assess, often on dangerous field trips, the effects of herbicide use during the Vietnam War.

Anton was born in St. Petersburg, Russia, on January 18, 1913. His father was a famous cardiologist of German ancestry; his mother was Russian. In the early summer of 1917, he and his mother went on one of their yearly summer vacations to the family dacha near the Finnish border. As the political situation in Russia worsened, the family council decided that Anton and his mother should move to Finland until the conditions in Russia normalized again. After four years of waiting in vain for this to happen, Anton moved with his mother to relatives in Germany, first to a small rural town in eastern Pomerania and then to Berlin.

Anton's early interest in plants was awakened by a school project. He studied the flowers of cucumbers and peas during one summer and at the age of eleven wrote a monograph on the topic. His interest in plants persisted and, after graduation from gymnasium, he enrolled in 1931 at the University of Berlin with botany as his major subject. While studying, he also served as an extra at the Berlin State Opera. For a short while, he even considered becoming an opera singer himself. However, after one audition with an uncle, this plan was dropped. Even though Anton was a very busy man in his later professional life, going to the opera and tending to his flower garden remained his favorite pastimes, as was reading in the three languages in which he was fluent: English, German, and Russian.

Geneticist Elisabeth Schiemann, one of the first women scientists to penetrate the German academic establishment, was Anton's thesis advisor. For his dissertation, he studied evolutionary problems in the genus *Stachys* using genetic and cytological approaches.

Being a stateless person in Germany was not an easy position in the Third Reich and this led to some tense situations for Anton, e.g., the initial refusal of the authorities to admit him to his doctoral exam. His efforts to leave Germany and to continue his studies abroad were unsuccessful. Since Anton did not have German citizenship, he was precluded from obtaining a scholarship and had to earn his way through the university. He did this in part by writing abstracts of papers for various scientific journals. This occupation, which was often tedious and dull, brought two benefits. First, it helped him later in his career to distill the essence of papers for his reviews that became classics in the field. Second, Anton's succinct abstract of a paper by Georg Melchers attracted the attention of the author, who offered him a position as scientific assistant at the Kaiser Wilhelm

Institute in Berlin-Dahlem after Anton's graduation in 1939. Melchers was one of the upcoming developmental plant biologists whose work, together with that of Chailakhyan in the Soviet Union, had led to the hypothesis that flowering is controlled by a hormone. The cooperation between Anton and Melchers proved extremely fruitful and continued at the Max Planck Institute in Tübingen until 1949, when Anton, his wife Lydia, and his mother emigrated to North America. Anton described these ten years with Melchers as one of the most exciting and cherished periods of his career.

Much of our understanding of photoperiodism and vernalization derives from that period of Anton's career. The years of collaboration with Melchers provided a firm physiological basis for the flower hormone (florigen) concept. According to this hypothesis, photoperiodic induction is perceived by the leaves, and a hormonal substance is then transported from the induced leaves to the shoot apex, where it causes a transition from vegetative growth to reproductive development. Using annual and biennial strains of Hyoscyamus niger (black henbane, later at Caltech referred to as Russian spinach) and short-day and day-neutral varieties of tobacco and the long-day plant Nicotiana silvestris, they showed that the graft-transmissible promoter of flower formation is similar, if not identical, in different species and different photoperiodic response types. However, efforts to extract the flower hormone failed. With self-deprecating humor, Anton used to say that he was a member of that distinguished group of plant physiologists and biochemists who had failed to isolate and identify the elusive floral hormone "florigen." Nevertheless, Anton remained an outspoken proponent of the hypothesis that a specific substance is required for the change from vegetative to reproductive development in plants. Anton and Melchers also studied vernalization in biennial Hyoscyamus, i.e., the effect

of cold-treatment on subsequent flowering. They showed that vernalization proceeded in two stages, the first reversible and the second not.

In the New World, Anton's first station was Montreal, where he was the recipient of a Lady Davis fellowship in the genetics department of McGill University. As his fellowship at McGill drew to a close, Anton accepted his first job in the United States, a visiting professorship at Texas A&M University. There, Anton was engaged in studies on the flowering of cotton. In the fall of 1950 Anton moved to Caltech, where he became a research fellow with James Bonner. His research with James Liverman addressed the effects of auxin on flowering. Of his two years in Pasadena, Anton said that no one who had passed through Caltech had left it quite the same person, and probably everyone retained a trace of regret at having left.

In 1952 Anton accepted a faculty position in the botany department at UCLA. His seven years at UCLA were among the most productive ones of his career. The growth-promoting effects of the newly recognized plant hormone gibberellin were already known at that time. However, all work had been carried out with plants that had already formed stems. In contrast, Anton applied gibberellin to rosette plants, i.e., plants without a developed stem and found "with boundless delight" that treatment with gibberellin elicited first stem elongation and subsequently flower formation. Although gibberellin was the first chemical to consistently elicit flower formation in vegetative plants, Anton was quick to point out that it was not the elusive florigen. Based on results of earlier grafting experiments, he reasoned that florigen appears to be the same in short- and long-day plants, whereas applied gibberellin can induce flower formation in longday plants, but not in short-day plants. Therefore, he concluded that gibberellin and florigen could not be the same.

However, he suggested that gibberellin may be involved in the formation of florigen in those plants in which applied gibberellin causes flower formation. Evidence in favor of this idea was obtained later.

Another important discovery at UCLA was that applied kinetin, another newly discovered plant hormone, delayed senescence of detached Xanthium leaves. This finding gave rise to the idea, later shown to be correct, that cytokinins fulfill the role of Chibnall's hypothetical root hormone. Such a substance was thought to be produced in the root and transported to the shoot where it would prevent processes associated with senescence, e.g., breakdown of protein and chlorophyll. Cytokinins were already known to regulate cell division when applied in combination with the phytohormone auxin. Anton's discovery that they also retarded leaf senescence opened a whole new field of research. As Anton stated, these various results provided so many leads for further work that it was necessary to decide which ones to follow. Since the effects of gibberellin were closer to the flowering problem, he decided to concentrate on the action of this plant hormone.

In 1959 Anton moved from UCLA back to Caltech, this time as professor of biology and director of the Earhart Plant Research Laboratory, called colloquially the "phytotron." This complex of climate-controlled greenhouses and growth chambers had been designed by Frits Went for the study of plant growth and development under various environmental conditions. In Pasadena, Anton continued his studies on gibberellin action. By that time, the structures of nine gibberellins were known, and Anton compared the effects of these on stem growth and flowering in several plants.

We, the authors of this memoir, were both postdoctoral fellows at Caltech and did at least part of our research with Anton. One important project in which we participated concerned the mode of action of a class of synthetic plant growth regulators, the so-called growth retardants. They were shown to specifically block gibberellin biosynthesis, thereby inhibiting those growth and developmental processes that require this hormone (e.g., flowering in Samolus and Bryophyllum). Anton was a supervisor who left his coworkers plenty of room for their own initiatives in research but he also instilled in each a sense of high standards regarding the choice and solution of scientific problems. The atmosphere at Caltech was one of continuous stimulation, since these were the days when modern molecular biology was being born. Nevertheless, trips to the desert, the mountains, and the sea were part of our lives, and seminars were sometimes devoted to travelogues, especially after conferences in faraway places. In Pasadena, we also experienced the wonderful hospitality of Anton and Lydia Lang. The Russian Christmas parties, later continued in East Lansing, were a tradition that we all cherished, especially a memorable one held in the Mexican style.

In 1964 the Atomic Energy Commission decided to build the Plant Research Laboratory at Michigan State University, and Anton was named its first director. He moved to East Lansing in 1965 and assembled as staff a group of young faculty members, which included both of us. Anton built an institution that still carries his imprimatur. The esprit de corps of the Plant Research Laboratory is largely a direct result of the philosophy that guided Anton's leadership. He did not have a personal agenda, but he demonstrated in many ways his total commitment to excellence in science. As one example, which director today would take the time to read and edit every paper written in his institute? At the Plant Research Laboratory, Anton initially continued his research on gibberellins, but once he became involved in

studying the effects of herbicide use in Vietnam his own research program came to a temporary halt.

After Anton completed his tour of duty in Vietnam, he returned to the bench—or, as he more accurately put it, to the greenhouse. During a sabbatical leave in Moscow with Chailakhyan, he demonstrated that graft-transmissible inhibitors of flower formation (antiflorigens) are formed in non-induced leaves, specifically of the long-day plants *Hyoscyamus niger* and *Nicotiana silvestris*. Following his official retirement in 1983, Anton continued to work on flowering, particularly on in vitro regeneration of flower buds from thin-tissue layers of tobacco. In his last publication, he showed that the potential for formation of flower buds is present in explants from flowering *Nicotiana* plants of all photoperiodic types, not just day-neutral ones.

Anton dedicated much of his time to editing and writing reviews. To many plant physiologists, he was best known for his work as managing editor of *Planta*, an international journal that attained eminence under his uncompromising leadership. The current editors of *Planta* wrote in their obituary that nothing escaped Anton's eagle eye. Authors, editorial board, managing editors, and Springer-Verlag would all receive lengthy letters setting out his comments and criticisms in definitive terms. As editor, Anton provided many young colleagues with meticulous lessons in scientific writing. We all learned, among other things, that results do not suggest, only people do; results indicate. Also, experiments do not reveal; revelations are reserved for the Bible. Anton's reviews were legendary, sometimes longer than the papers themselves. Anton was an intellectual with little flair for technology. He used to type his reviews with two fingers on an old-fashioned typewriter, and Lydia typed the clean copy. One of us offered to teach Anton and Lydia the essentials of word processing, which would have saved both of them a lot of time. Anton gave a stern look and replied, "Lydia and I do not want to save time." As every secretary in the Plant Research Laboratory would confirm, Anton was a democratic man. He insisted on making his own photocopies, just like everybody else did. However, as the photocopiers became more and more sophisticated, his war with this equipment kept escalating. Anton was much better at writing incisive papers than at pushing buttons.

Between 1941 and 1961 Anton also wrote annual reviews on developmental plant physiology in *Fortschritte der Botanik* (now *Progress in Botany*). His writings were never mere compilations of the newest literature but always an integration of new information with earlier work and hypotheses. He also undertook the monumental task of editing volumes XV/1 and XV/2 of the *Encyclopedia of Plant Physiology*. Despite the fact that there were more than fifty contributing authors, these two volumes are among the best edited and integrated ones in this series. Anton's own article "Physiology of Flower Initiation" remains one of the most thorough and comprehensive reviews on flowering. Anton also served on editorial boards of other journals, e.g., of *Plant Physiology*, *Developmental Biology*, and the *American Journal of Botany*.

Anton's sense of duty was tested to the limits when he was asked to chair the National Academy of Sciences Committee on the Effects of Herbicides in South Vietnam. During the Vietnam War, herbicides were used by American forces to defoliate dense forests, thereby facilitating detection of North Vietnamese and Viet Cong military units. To a lesser extent, herbicides also were used to destroy crops. As the magnitude of this program increased, critical voices were heard, and Congress directed the Secretary of Defense to ask the National Academy of Sciences for a study on the ecological and physiological effects of herbicide use in Vietnam. The Academy accepted this responsibility and

in early 1971 Anton agreed to chair the committee despite serious concerns over the feasibility of this task. He did so because he believed in the importance of determining the nature and scale of these effects, and because delaying this assessment lessened the prospects of obtaining meaningful data.

To increase the credibility of the committee, Anton insisted on the inclusion of foreign experts. This request was granted, even though the committee had to deal with classified information at a time when the war was in full progress. Accordingly, the National Academy of Sciences Committee on the Effects of Herbicides in South Vietnam included. besides nine U.S. scientists, three from the United Kingdom, two from Vietnam, and one each from Canada, Sweden, and Taiwan. The obstacles in carrying out the study and writing a report were formidable. They ranged from collecting quantitative field data under combat conditions to dissent among members of the committee on the evaluation of some of the data. Anton and members of the committee came under fire while conducting aerial surveys of herbicide-treated forests and had to endure many physical hardships during their research in the field.

Nevertheless, the committee was able to make estimates of the ecological and health consequences of massive herbicide applications over wide areas. It issued a voluminous report that was submitted by the Academy to Congress and the Secretary of Defense in 1974. This initial study lacks, for obvious reasons, follow-up investigations that would have been necessary to verify the original data and to assess the long-term effects of herbicide use on forest ecology and human health. Anton undertook this assignment because of his deeply felt loyalty to the United States and the National Academy of Sciences. In his recollections published as a prefatory chapter in the 1980 volume of the *Annual* *Review of Plant Physiology*, Anton stressed the values of positive patriotism, namely attachment to and pride in one's country. It goes without further elaboration that Anton also served on numerous national committees and panels of the Academy, the National Science Foundation, and other federal agencies.

Anton's scientific and civic contributions were widely recognized, and he received many national and international awards. Among them were in 1976 the Stephen Hales Award and the Charles Barnes Life Membership Award of the American Society of Plant Physiologists. This came as a great surprise to him because nobody before (and since) had received these two highest honors of the Society at the same time. In thanking the selection committees, Anton wrote, "A person adapted to Russian winters, German cuisine, Canadian French, Californian smog, Southeast Asian sniper bullets and other major natural disasters can stand such a stress-but can somebody else, e.g., a plain American?" In 1965, Anton was elected to the German Academy of Natural Scientists (Leopoldina), in 1967 to the National Academy of Sciences, and in 1968 to the American Academy of Arts and Sciences. In 1981 he received an honorary doctorate from the University of Glasgow, and in 1982 he was awarded an honorary membership by the German Botanical Society. He was elected president of the Society for Developmental Biology in 1968 and of the American Society of Plant Physiologists in 1970.

Anton is survived by his wife Lydia who supported him in all of his professional activities. She was a wonderful hostess to all visiting scientists, a true "first lady" when Anton was director of the Plant Research Laboratory, and an efficient editorial assistant. His family includes his two sons

Peter and Michael; his daughter Irene; Irene's husband Howard Kleiman and their children Joshua and Carly.

In conclusion, we want to recognize Anton in the words of a member of the committee that selected him for the Charles Barnes Life Membership Award: "I have a personal affection for Anton Lang because of his selfless contributions to all of us in plant physiology. His personal warmth, kindness and concern for the welfare of young and littleknown scientists have helped along many careers, including my own." This is how we and his colleagues will remember him.

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