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SHANG FA YANG
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A Biographical Memoir by
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SHANG FA YANG WILL BE remembered as the plant biochemist who elucidated the pathway for the biological synthesis of ethylene, a plant growth-regulating hormone. Ethylene, a simple compound containing two carbon and four hydrogen atoms, was known already in the early 20th century to elicit abnormal growth in plants and to hasten the ripening of fruits. This remained somewhat a curiosity associated with leaking gas mains until it was shown in the 1930s that plants produce ethylene and that it is broadly involved in regulating plant growth and development, including seed germination, root and shoot growth, responses to environmental stresses, flowering, fruit ripening, and senescence or death of plant tissues and organs. The fact that ethylene is a gaseous compound made it unique among plant hormones, and it was of considerable interest to understand the mechanism and biochemical pathways by which plants produced the compound.

At the time Yang entered the field there was some evidence that the amino acid methionine could be a precursor for ethylene production, and various in vitro systems were being explored to convert this and other potential precursors into ethylene. Yang contributed significantly to these studies, using his knowledge of chemistry to explore different reaction mechanisms. Eventually, however, it was in vivo studies that led to the breakthrough when Yang's group supplied apple fruit tissues with ^{14}C-labeled methionine and observed that a labeled compound accumulated under anaerobiosis, a condition that prevents ethylene synthesis. They identified the compound as 1-aminocyclopropane-1-carboxylic acid, or ACC, and showed that it could be readily converted to ethylene by plant tissues under aerobic conditions. This discovery led to the identification of the enzymes responsible for production of ACC from S-adenosylmethionine (SAM) and for conversion of ACC to ethylene, their eventual cloning and characterization, and opportunities for the genetic and chemical manipulation of ethylene biosynthesis and action in plants. Yang also discovered that the methylthioribose group from SAM is recycled back into methionine formation following ACC synthesis to sustain high rates of ethylene production, which has been termed the "Yang Cycle." In addition, he studied cyanide metabolism (after discovering that cyanide is a by-product of ethylene biosynthesis) and the effects of sulfur dioxide on plant cellular processes.

The elucidation of the ethylene biosynthetic pathway and the enzymes involved stimulated many studies of how this pathway is regulated in plants by both internal and external factors. The specific roles of different gene family members encoding the ethylene biosynthetic enzymes have been elucidated for a number of important plant growth stages. Yang's work focused attention on ethylene in plant biology, subsequently resulting in the first identification of a plant hormone receptor and a detailed understanding of the molecular signaling pathways by which ethylene is perceived in plant cells. Yang also contributed to the development of ethylene-releasing compounds that allow the convenient application of ethylene to promote fruit ripening or to facilitate harvest. He helped to develop chemical antagonists that block ethylene action and are now used commercially to extend the life of cut flowers. This dual focus exemplifies Shang Fa Yang's scientific contributions: rigorous studies of fundamental mechanisms in plant biochemistry and the simultaneous application of that knowledge to solve problems in crop production and storage.

Shang Fa Yang did not know the exact date of his birth in Taiwan but deduced that it was in late October or early November of 1932; he celebrated his birthday on November 10. He was the youngest child of a large family (five elder brothers and six elder sisters). His father, Chian-Zuai Yang, was a businessman involved in the production of maltose from sugarcane in Tainan City, but the factory was sold in 1936 and his father became a miller. Yang entered primary school when he was seven years old and began to learn Japanese, as Taiwan was under Japanese control at that time. Every morning, students assembled for a speech by the Japanese head of the school, who exhorted them to grow strong to beat the Americans. Yang's mother died when he was in the fifth grade, and his third eldest sister took care of him afterward. Near the end of 1944 American aircraft began to bomb Taiwan and air raid alarms were frequently heard. Yang noted that he particularly remembered March 1, 1945, when the city was bombed and houses were burning. He took refuge in a bomb shelter with friends and emerged later to discover that a 500-kg bomb had created a crater only about 500 meters from their shelter. He considered himself very lucky to have escaped injury. His family then moved to the countryside but returned to Tainan City after the Japanese surrender in August 1945. However, life was very difficult due to food shortages. Rice was expensive and hard to find, and their main food was radishes. He resumed middle school in 1946, still using Japanese and starting to learn Chinese. Armed soldiers from mainland China were in the streets and the situation in Taiwan remained dangerous for several more years. When he was in senior high school, Yang also lost his father.

Yang entered National Taiwan University in 1952 and studied agricultural chemistry because he wanted to help the farmers and thus promote agriculture in Taiwan. Although food remained in short supply and his nutrition was poor, Yang was active as a leader of student organizations. He received his B.S. degree in 1956 after writing a 40-page research report in English, and subsequently completed an M.S. degree, also in agricultural chemistry from the National Taiwan University, in 1958. Although funding for research was limited, Yang was highly motivated and initiated independent studies with the support of his professors. When he discussed his research with his colleagues and professors, he used a mixed language of Japanese, Taiwanese, and Mandarin. Reference books from Japan were much cheaper than the books from the United States, so he read many biochemistry journals in Japanese. Yang remained sufficiently fluent to present seminars in Japanese when he was invited to Japan in his later years. He also was asked to learn German before he got his M.S. degree. He studied hard and passed his exam, but did not claim to be good in German. He planned to study abroad, and in consequence was also required to undertake four months of basic army training before being allowed to leave.

Yang received a scholarship to study in the United States, where he attended Utah State University and worked with G. W. Miller on the effects of fluoride on plant biochemistry and metabolism (Yang and Miller, 1963), receiving his Ph.D. in 1962 in plant biochemistry. He then pursued postdoctoral research with Paul K. Stumpf at the University of California, Davis, where he studied lipid biosynthesis in avocado fruits (Yang and Stumpf, 1965). He then accepted a postdoctoral fellowship with B. N. LaDu at New York University Medical School in 1963-1964 but determined that he did not like working with animals or living in the city. However, not all was lost, as he met Eleanor Liu, an accounting student at NYU, who subsequently became his wife in September 1965. He returned to California and to plant biochemistry in 1964 as a postdoctoral scientist with Andrew A. Benson at Scripps Institution of Oceanography in La Jolla. In 1966 Yang was hired as an assistant biochemist in the Department of Vegetable Crops at the University of California, Davis, and immediately began studies of the plant hormone ethylene that would be the focus of his scientific career.

Yang was hired to conduct research on the postharvest biochemistry of fruits and vegetables, a topic of considerable importance to the horticultural industry in California, which ships fresh produce long distances to markets in the eastern United States and internationally. He initially shared a laboratory in the newly constructed Mann Laboratory with Harlan K. Pratt, a pioneering researcher in the ethylene physiology of fruits. The gaseous compound was known to hasten the ripening of fruits and to cause growth distortions in growing plants, and had been shown in 1934 to be produced by ripening fruits. Pratt had constructed a gas chromatograph that could measure the parts-per-million concentrations of ethylene produced by plants and had demonstrated the close relationship between ethylene and fruit ripening. However, little was known about the pathway of ethylene biosynthesis in plants, and Yang set out to apply his biochemical expertise to this aspect of plant ethylene biology.

The modern search for the ethylene biosynthetic pathway began in 1965 when Morris Lieberman's group discovered that both plants and in vitro chemical systems converted methionine into ethylene. Yang's first paper on ethylene (1966) explored the intricacies of an in vitro model system for the generation of ethylene from methionine, and he utilized both in vitro and in vivo approaches to explore potential intermediates of and mechanisms for the conversion of methionine to ethylene (1972; Baur and Yang, 1969). He also studied the mechanism of formation of ethylene from 2-chloroethylphosphonic acid in plant tissues (Yang, 1969; Yamaguchi et al., 1971). This compound, under the generic name of ethephon, enabled the commercial application of ethylene for agricultural purposes, as it is taken up by plants and converted into ethylene. It has been widely used as a fruit-ripening agent, to loosen fruits for harvest and for defoliation of cotton before harvest.

Continuing studies on the biogenesis of ethylene showed that methionine was converted to S-adenosylmethionine (SAM) and that SAM was a precursor of ethylene. In addition, under anaerobic conditions that prevented ethylene formation, a labeled compound accumulated in tissues supplied with ^{14}C-SAM (1977). This discovery stimulated active competition among various groups to identify the unknown intermediate between SAM and ethylene. This intensive effort culminated in the identification of 1-aminocyclopropane-1-carboxylic acid (ACC) as the immediate in vivo precursor of ethylene (1979[1]). Yang quickly developed a sensitive assay for ACC via its chemical conversion to ethylene (1979[2]), which facilitated wide-ranging studies by his group on the regulation of ACC and ethylene biosynthesis in plant growth, fruit ripening, and stress responses (1980[1,2]; Hoffman and Yang, 1980; Yang et al., 1980).

With the identification of the two key steps in ethylene biosynthesis, the conversion of SAM to ACC and of ACC to ethylene, Yang turned his attention to the identification of the enzymes responsible for them. His group and that of Hans Kende at Michigan State University soon reported the isolation of 1-aminocyclopropane carboxylate synthase, the enzyme responsible for the conversion of SAM to ACC (1979[4]; Boller et al., 1979). Isolation of the ethylene-forming enzyme, or ACC oxidase, was a more difficult task, and many studies of ACC metabolism were conducted in conjunction with this search. Yang's group determined that ACC could be malonylated and that this pool of conjugated ACC was largely unavailable for conversion to ethylene (1982[1]). Light, carbon dioxide, oxygen, and water stress all influenced the conversion of ACC to ethylene (reviewed in 1984[1]). The conversion of ACC to ethylene was also stereospecific, as demonstrated by the differential conversion of stereoisomers of 1-amino-2-ethylcyclopropane carboxylic acid to 1-butene (1982[2]). This provided an important test for the enzymatic conversion of ACC to ethylene versus non-specific chemical conversion (McKeon and Yang, 1983) that was important in the subsequent isolation of ACC oxidase (1992). Additionally, Yang's group demonstrated that cyanide was a by-product during the enzymatic conversion of ACC to ethylene (1984[2], 1988). Under conditions involving high rates of ethylene synthesis, such as following induction by auxin or during fruit ripening, the cyanide detoxification enzyme L-3-cyanoalanine synthase removes cyanide resulting from the oxidation of ACC, thereby maintaining a safe level of cyanide in these tissues (1988).

These metabolic studies also revealed that methionine pools were too low in plant tissues to sustain the observed rates of ethylene synthesis. Yang's group demonstrated that after ACC is released from SAM, the methylthioribose moiety from the remaining methylthioadenosine is recycled to replenish methionine levels and sustain ethylene biosynthesis (Miyazaki and Yang, 1987). Some had speculated that the methylthio group would simply be attached to an existing homocysteine molecule to form a new methionine molecule, thus recycling only the methylthio group. Yang's research confirmed that both the methylthio group and ribose carbons from methylthioadenosine became part of the newly formed methionine. The reactions of this recycling pathway (Yang et al., 1990) were known in other systems (bacteria, yeast, rat liver extracts), but Yang's group was the first to demonstrate that it was active in plants, and it has been christened the "Yang Cycle" in plant biochemistry textbooks.

As the tools became available for cloning and characterizing the genes responsible for the steps in ethylene biosynthesis, Yang contributed to many studies of the regulation of those genes in fruit ripening, plant growth, wounding, and stress responses (1991; 1994; Yip et al., 1992; Shiu et al., 1998; Yang and Oetiker, 1998). Particularly noteworthy were his studies of the active sites and mechanisms of action of ACC synthase and ACC oxidase (1990; Li et al., 1996; Shaw et al., 1996; Zhou et al., 1999; Charng et al., 2001). Yang wrote numerous highly cited reviews and book chapters that defined ethylene biosynthesis and its role in plant biology for a generation of students and researchers (Yang, 1980, 1984[1], 1985).

While most widely known for his work on ethylene biosynthesis and action, Yang also maintained active research programs in other areas of plant growth and metabolism, including on auxin metabolism and action (1979[3]; Aharoni and Yang, 1983), cytokinin action (Lau and Yang, 1973; Chen et al., 2001), and the biological effects of sulfite and sulfur dioxide (Peiser and Yang, 1979, 1985).

In all his work Yang continually linked his discoveries to practical applications in postharvest biology and plant growth regulation. He applied his knowledge of chemistry and physiology to learn more about ethylene biosynthesis, and he utilized this information to improve postharvest storage conditions and product quality (Hyodo et al., 1978; Yang, 1987; Yang and Oetiker, 1998). His knowledge of the literature related to ethylene and plant hormones was encyclopedic, and he was continually testing and retesting fundamental mechanisms and interactions as new data became available. Yang was a rigorous but positive mentor and role model to his graduate students and postdoctoral associates and actively encouraged and assisted them in obtaining positions and advancing their careers.

Shang Fa Yang traveled extensively, including sabbatical leaves in Germany, Taiwan, the United Kingdom, and Japan. He figured prominently at many national and international research conferences and served on the editorial boards of leading journals and as a member of several professional and scientific societies. He won many awards and honors, including the Campbell Award of the American Institute of Biological Sciences in 1969, a Guggenheim Fellowship in 1982, the International Plant Growth Substances Association Research Award in 1985, and the Outstanding Researcher Award from the American Society for Horticultural Science in 1992. Yang was named the University of California, Davis, Faculty Research Lecturer in 1992, the highest honor given by this institution for excellence in research. He was elected to the National Academy of Sciences in 1990 and to the Academia Sinica in Taiwan in 1992. In 1991 Yang received the prestigious international Wolf Prize in Agriculture, often considered to be the "Nobel Prize" for agricultural research.

After an outstanding career as professor and biochemist at the University of California, Davis, Yang took early retirement in 1994 to accept a Distinguished Professorship at the Hong Kong University of Science and Technology (HKUST), where he established an active plant research group in the Department of Biology. He continued his work on ethylene, particularly on the characterization of the structure and function of ACC synthase (2000; Li et al., 1996; Zhou et al., 1999). He also coedited a book on *Discoveries in Plant Biology* with his colleague S. D. Kung at HKUST (Kung and Yang, 1998). In 1995 Yang was recognized as a Distinguished Research Fellow by the Institute of Botany of the Academia Sinica in Taipei, Taiwan. He returned to Taiwan in 1996 to serve as the director of the Institute of Botany and subsequently as vice president of Academia Sinica from 1996 to 1999. In this position he directed its numerous research institutes, including the establishment of the new Institute of Agricultural Biotechnology (subsequently renamed the Agricultural Biotechnology Research Center). He also served as the first chief director of the National Science and Technology Program for Agricultural Biotechnology, which funds and oversees research and development projects related to agricultural biotechnology in Taiwan. Yang played important leadership roles in advancing plant biology and agricultural biotechnology in both Hong Kong and Taiwan. Following his service with Academia Sinica, Yang retired to Davis, California, although he continued to publish additional scientific work.

Shang Fa Yang passed away suddenly and unexpectedly from complications of pneumonia on February 12, 2007, at the age of 74. He is survived by his wife, Eleanor, and two sons, Albert and Bryant, who have pursued careers in engineering and chemistry, respectively. Prior to his death, Yang was planning to endow a program to foster greater scientific exchange between the University of California and the Academia Sinica. This initiative was continued by Eleanor, Albert, and Bryant, and culminated in the establishment of the Shang Fa and Eleanor Yang Scholarly Exchange Endowment in October 2007. This endowment will support visits of scholars in the agricultural, biological, and chemical sciences between the University of California, Davis, and Academia

Sinica, Taiwan, two institutions that Shang Fa Yang loved and served with distinction.

Shang Fa Yang's contributions to plant biology, including his discovery of the pathway for ethylene biosynthesis, the elucidation of the Yang Cycle and his work on auxin, sulfur, and cyanide metabolism, are described in more than 225 journal articles and book chapters that he published during his career. He has earned a significant and enduring place in the modern history of plant biochemistry. His humor and humanity endeared him to students, colleagues, and friends, who also appreciated and benefitted from his remarkable intelligence. His untimely death prematurely ended a life devoted to scholarship, teaching, and service.

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