BIOGRAPHICAL MEMOIRS

WILLIAM S. BOWERS

December 24, 1935 – June 23, 2021 Elected to the NAS, 1994

A Biographical Memoir by David L. Denlinger and Lynn M. Riddiford

THE FIELDS OF insect endocrinology and chemical ecology have many heroes, but few have contributed game-changing findings as fundamental as the contributions of William S. Bowers. Although it was known that insects produced some sort of hormone responsible for maintaining the juvenile status, it was Bowers who synthesized the first highly active juvenile hormone (JH) analog and thus launched the use of JH and its many analogs and antagonists for practical use in pest management. Also, while it was known that aphids communicated through some sort of chemical signals, it was Bowers who came up with the identity of the alarm pheromone. His deep understanding of biology and chemistry provided a powerful platform for making major advances in the insect sciences.

William Sigmond Bowers was born December 24, 1935, to William and Florence Bowers in the small farming town of Decatur, Indiana, where his parents operated Bowers Hardware Store. He attended St. Mary's Elementary School and graduated in 1953 from St. Joseph's High School, where he became interested in science. He attended Marquette University for two years and then transferred to Indiana University to complete his undergraduate education. A class in entomology during his senior year enticed him to pursue a career in the insect sciences. After receiving his bachelor of arts degree in zoology and chemistry from Indiana University, he obtained his Ph.D. in 1962 from Purdue University, with specialties in entomology, biochemistry, and physiology.

Upon completing his graduate studies, Bill accepted a position as an insect physiologist at the USDA Pioneering



William S. Bowers, photo courtesy of University of Arizona.

Research Laboratory in Beltsville, Maryland. It was there that he began his research on the development of biorational strategies for plant and public health protection, focusing on insect growth and behavior-regulating allelochemicals. In 1965, he synthesized an analog of JH that had activity comparable to the natural hormone from the *Cecropia* silkmoth. Later it turned out that this compound was the natural hormone in most insects. His findings led to his being named the Outstanding Young Scientist by the USDA in 1969 and again in 1970.



NATIONAL ACADEMY OF SCIENCES

©2024 National Academy of Sciences. Any opinions expressed in this memoir are those of the authors and do not necessarily reflect the views of the National Academy of Sciences. In 1972, Bill became a professor of entomology and chemical ecology at Cornell University's campus in Geneva, New York. He continued his research interests in insect endocrinology, and shortly after arriving in Geneva, he began searching for anti-juvenile hormones in plants. These studies will be discussed in more detail below. During this period in his life, Bill also began his service as a visiting director of research at the International Centre of Insect Physiology and Ecology (ICIPE) in Nairobi, Kenya, an assignment that required frequent visits to Kenya to help guide research projects at ICIPE.

A move to the University of Arizona in 1984 as head of the Department of Entomology allowed Bill to assemble a faculty of world-renowned insect scientists. He was instrumental in establishing the Center for Insect Science, a National Science Foundation-designated Biological Center of Excellence. The center was highly successful in recruiting not only outstanding faculty but an impressive cadre of talented graduate students and postdocs. He was selected as a Fulbright Scholar in 1987 and spent six months as a visiting scientist at Assiut University in Cairo, Egypt.

Bowers's stellar research accomplishments led to numerous awards in addition to his election to the National Academy of Sciences in 1994. He received the J. Everett Bussart Memorial Award from the Entomological Society of America in 1980; the Alexander von Humboldt Award in 1989; the Founders Memorial Award from the Entomological Society of America in 1991; the President's International Scholar Award from Assiut University, Cairo in 1993; the Distinguished Alumnus Award from the College of Agriculture at Purdue University; the Kenneth A. Spenser Award from the American Chemical Society in 1994; the Silver Medal Award from the International Society of Chemical Ecology; and the Sterling B. Hendricks Award from the American Chemical Society in 2000. He was elected a fellow of the Entomological Society of America in 1996 and the American Association for the Advancement of Science in 1999.

Following a sabbatical at Queensland University in Adelaide, Australia, Bowers retired from the University of Arizona in 2002. As a professor emeritus, his curiosity and love for science persisted. He followed science news daily throughout his retirement years, and many of us were recipients of his candid assessments of current developments in both the scientific and the general state of the world!

Bill had numerous interests beyond his scientific endeavors. Always an avid gardener, he spent many happy hours planning, planting, and harvesting his crops and produced great tomatoes and peppers every year, wherever his garden happened to be. The vineyard he planted in New York produced grapes from which he made fine wines. In Arizona, olives captured his interest. Both green and black olives were harvested and processed from the trees he planted.

It was during his studies at Indiana University that a young student nurse "danced" into his life. He shared his love and life with Patricia as his wife for sixty-three years. Together they enjoyed many travels by RV, boat, plane or pickup truck, journeys that took them to exciting places around the world. Bill was father to sons Marc (deceased) and Rion and daughters Dana, Erin, and Lisa and grandfather to five grandchildren: Leslie, Ryan, and Caroline Thompson, and Daniel and Emily Bowers.

LAUNCHING THE USE OF INSECT HORMONES FOR PEST MANAGEMENT

Juvenile hormone (JH) has two major functions in insects: (1) prevention of metamorphosis until the nymph or larva is large enough and (2) gonadotropic action in the adult female. In the early 1960s, before the chemical structure of JH was known, Bowers found several farnesol derivatives that prevented metamorphosis of the beetle *Tenebrio molitor* and had gonadotropic action in the cockroach *Periplaneta americana*.¹ He then went on to synthesize an extremely active farnesenic acid derivative that later turned out to be JH III, the natural hormone in most insects.² He also found that several known synergists for insecticides had JH activity in their own right.³

In 1964, Sláma and Williams found that American paper products prevented metamorphosis of the linden bug *Pyrrhocoris apterus* but not of a related species, the milkweed bug *Oncopeltus fasciatus*. Moreover, the active substance could be extracted from the balsam fir. Bowers identified the active compound from the balsam fir as the methyl ester of todomatuic acid, which he called "juvabione."⁴ These findings indicated that hormonal analogs could act selectively on particular species of insects and started the field of insect growth regulators (IGRs).

After spending several years synthesizing more effective JH mimics to be used for insect control, Bill began a search for anti-JHs from plants. He focused on compounds that would cause precocious metamorphosis and prevent normal reproductive maturity in females, and he used the milkweed bug for his bioassays. From the common bedding plant *Ageratum houstonianum*, he extracted two chromene derivatives that he called precocenes.⁵ These compounds proved to be cytotoxic specifically to the cells of the corpora allata, thus causing the degeneration and inability of these endocrine glands to produce JH, resulting in miniature adults that could not produce eggs.⁶ He then went on to show that precocenes had similar effects in other hemimetabolous insects. They were not effective in causing precocious metamorphosis in holometabolous insects, however.

Bowers continued looking for hormonally active substances from plants. In 1980, he identified two extremely potent JH mimics that he named juvocimenes in sweet basil that were highly active in *Oncopeltus*.⁷ He also found that plants can increase their production of 20-hydoxyecdysone (20E; the active insect molting hormone) in response to insect herbivory.⁸ The 20E deters more feeding, thus protecting the plant. Further studies showed that a similar defense strategy is used by plants infected with parasitic nematodes. In this case, the molting of the nematode is disrupted.⁹

CHEMICAL COMMUNICATION IN APHIDS

Although Bowers is perhaps best known in entomological circles for his work on JH mimics and precocenes, his early work on aphid alarm pheromones is equally notable and again reflects how he was able to parlay his skills in chemistry to solve an exciting problem in insect communication. This achievement also goes back to his early days as a USDA scientist working in his Beltsville laboratory.

Like many fun ventures in scientific discovery, his work with aphid alarm pheromones involved a bit of serendipity.¹⁰ Lowell "Skip" Nault invited Bowers to give a seminar at the Ohio State University, and with a bit of time to kill before catching his flight home, Skip showed Bill his aphid colonies. Skip, a superb insect behaviorist, was investigating the impressive alarm response elicited when a pea aphid (*Acyrthosiphon pisum*) detects danger. By crushing an aphid with his finger and bringing the finger near a cluster of aphids, Nault demonstrated to Bowers the alarm response—the aphids quickly fold their legs, drop from their feeding site, bounce off the lower leaves of their host plant, drop to the floor, and rapidly disperse. This dramatic demonstration elicited an unrepeatable response from Bill, and he immediately offered to find the chemical responsible.

A few months later, after Bowers returned to Beltsville, a USDA colleague collected a big batch of cotton aphids that had invaded one of their greenhouses. Bowers shipped Nault vials of extracts he had separated by chromatography. One of the four vials contained a chemical that elicited utter chaos when the aphids got their first "sniff." Nault capped the vial with the potent substance, sent it back to Bowers for further purification, and within six weeks of their initial interaction, Bowers and his colleagues identified and synthesized the pheromone. Six weeks later the identity of the alarm pheromone, a sesquiterpene, E- β -farnesene, was published.¹¹

The collaboration between Bowers and Nault resulted in numerous papers describing the effect of this sesquiterpene on a range of aphid species, and a number of analogs were developed with the goal of finding chemicals that would persist longer in the field and could potentially be used for plant protection. Although the alarm pheromone work did not result in commercial applications, the chemistry and biology of the response filled an intriguing gap in our knowledge of chemical communication and nicely demonstrated how Bill Bowers brought his skills in chemistry to bear in addressing exciting biological questions.

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WILLIAM S. BOWERS

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