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STANLEY D. BECK
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A Biographical Memoir by

JOHN L. WEDBERG, G. MICHAEL CHIPPENDALE,

AND JOHN C. REESE

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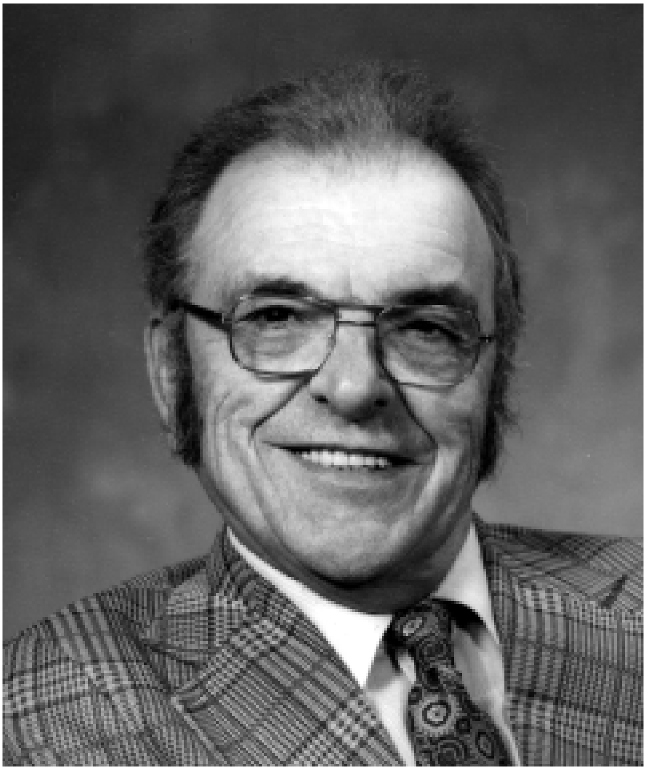

Stanley D Beck

STANLEY D. BECK

October 17, 1919–July 8, 1997

BY JOHN L. WEDBERG, G. MICHAEL CHIPPENDALE,
AND JOHN C. REESE

PROFESSOR STANLEY D. BECK was one of the last of the "Renaissance insect physiologists." A multifaceted researcher and educator, his major interests comprised three quite different areas of insect physiology. He made major contributions to host plant resistance to insects, especially maize resistance to the European corn borer, *Ostrinia nubilalis* (Hübner). With *O. nubilalis* and *Agrotis ipsilon* (Hufnagel) he studied the photoperiodic determination of insect development and diapause, as well as a long-term inquiry focused on particular circadian rhythms. Neither plant resistance nor insect photoperiodism/thermoperiodism could have been investigated in such depth without the foundation he laid years earlier with the development of nutritionally adequate artificial diets for insects. Beck's major scientific treatises included *Animal Photoperiodism* in 1963 and *Insect Photoperiodism* in 1968 (followed by a second edition in 1980), as well as two especially significant reviews on plant resistance and on insect photoperiodism (Beck, 1965; Beck, 1983).

PERSONAL HISTORY

Stan Beck was born on October 17, 1919, in Portland, Oregon. He grew up in several small towns in the state of Washington near Mount Rainier. As a young person he loved to hike and fish in the Cascade Range, and some of his funnier stories dealt with outwitting the wildlife agents in order to hike back to some of the best fishing spots. In an early biology course he became fascinated with insects, an ambition that directed him to Washington State University. He worked at a lumber mill for a year and in the apple orchards of an experiment station at Wenatchee, Washington, for two summers to earn money to attend college. He graduated magna cum laude and as a member of Phi Beta Kappa from Washington State University in 1942. He served as a lieutenant in the U.S. Navy on a minesweeper from 1942 to 1945. Stan started as a research assistant at the University of Wisconsin, Madison, in 1946, served as instructor of entomology from 1948 to 1950, and then as assistant professor of entomology after he received his doctorate in zoology in 1950. In 1952 Stan was stricken with polio, and after a 45-year struggle he succumbed to post-polio syndrome on July 8, 1997. Although polio left him confined to a wheelchair for the remainder of his life, his determination and courage did not allow this confinement to hinder his enjoyment of life.

His incredible list of accomplishments led to Stan's election to the National Academy of Sciences in 1988. He retired from the Department of Entomology, University of Wisconsin, Madison, in 1989. In retirement he was able to fulfill his lifelong dream of writing fiction; he published a novel, *Two in the Game,* about the difficulties of a dual-career family in academic life. He had also completed a draft of a mystery at the time of his death.

Stan is survived by his wife, Isabel, who worked tirelessly to make sure that he was able to travel and work, and to have a loving, caring family. He is also survived by a son, Bruce; two daughters, Diana Beck and Marianne Goins; and five grandchildren. He was preceded in death by a daughter, Karen Beck.

RESEARCH AND TEACHING CONTRIBUTIONS

Stanley D. Beck made enormous contributions to both science and philosophy. He published 138 refereed research papers; several books, including *The Simplicity of Science, Animal Photoperiodism, Insect Photoperiodism* (two editions), and *Modern Science and Christian Life;* and articles for scientific magazines. As noted by DeFoliart (2000) Beck had many firsts. He was the first to develop an artificial diet on which a phytophagous chewing insect could be reared for successive generations, the first to formulate an artificial diet for a phytophagous piercing-sucking insect, the first to clearly show the roles of various nutritional and allelochemic factors in the establishment and survival of insect larvae, and the first to demonstrate the role of growth-inhibiting allelochemics in plant resistance to insects. These discoveries laid the groundwork for many years of his research and opened the door for many other researchers.

Stan Beck's teaching largely concerned his courses in insect physiology and a proseminar course designed to assist graduate students in their written and oral presentations of scientific information. In this latter course he was known as a witty, cogent, and fluent speaker. He served as advisor for 18 graduate students, as well as a number of postdoctoral fellows, many of whom went on to distinguished careers in research, teaching, and administration. In all facets of his teaching he injected a little philosophy along with a lot of science. No matter how many times he had taught a given topic, he always reviewed his notes one more time just before heading down to the lecture room. He wanted his graduate students in his laboratory to come to him with ideas for experiments, rather than his outlining steps for students to carry out.

"As greater understanding of insect and plant biology, chemistry, and ecology is attained, we will be able to approach the goal of developing agronomic plants that are deliberately and foresightedly designed to be insect-resistant" (Beck, 1965). In that one sentence Beck was able to set the stage not only for many careers worth of research but also for the whole era of biotechnology in crop plants. Transgenic plants like Bt corn are certainly "deliberately and foresightedly designed to be insect resistant."

However, each step in science is built on the foundation of previous work. Before the explosion of work on the chemistry of plant resistance to insects could occur, artificial diets for the bioassay of plant allelochemicals had to be developed. Since then, artificial diets have been used for producing large numbers of insects for screening germ plasm, and have been particularly useful in the bioassay of resistance factors from plants. The advent of artificial diets also made it possible to investigate fundamental aspects of insect nutrition; one putative nutrient at a time could be deleted from experimental diets. In this way, for example, the essentiality of ascorbic acid for a lepidopterous insect was first demonstrated (Chippendale and Beck, 1964).

Bottger (1942) attempted to rear European corn-borer larvae on an artificial diet. Beck and Chippendale (1968) found that the larvae could not grow and develop unless there was microbial contamination. Beck and coworkers were the first researchers to develop an adequate artificial diet for a lepidopterous species, identifying critical components unidentified by previous researchers (Beck et al., 1949; Beck and Stauffer, 1950). The rearing of lepidopterous insects started with the 1949 and 1950 papers on successful artificial diets for rearing the European corn borer. These agarbased diets, incorporating both crude plant materials and specific nutrients, laid the foundation for countless projects. The contribution made by the development of artificial diets for lepidopterous species cannot be overemphasized. This beginning made it possible for the first time to investigate insect nutrition. Many detailed studies were to follow (Beck and Stauffer, 1950; Beck, 1950; Beck, 1951; Beck, 1953; Beck, 1956a; Beck, 1956d; Beck, 1957a; Casida et al., 1957; Scheel et al., 1957; Beck and Kapadia, 1957; Chippendale and Beck, 1965; Chippendale et al., 1965; Beck and Chippendale, 1968; Beck et al., 1968), demonstrating finally the importance of water itself as a nutrient (Reese and Beck, 1978).

Using the European corn-borer diet as a tool, Stan conducted the first systematic studies of the chemical basis of plant resistance (Beck, 1957b; Beck and Smissman, 1960). The availability of an artificial diet made it possible for the first time to assess large numbers of serial extracts and later, pure compounds, one extract or compound at a time. Beck's approach of serially fractionating the resistant plant became the model for systematic investigations. Rather than empirically testing hypothesized resistance factors and generating correlational evidence, cause-and-effect relationships could now be clearly documented. In this way three compounds were isolated from first-generation European corn-borer-resistant corn varieties (Beck and Stauffer, 1957). Originally these factors were designated Resistance Factors A, B, and C, or RFA, RFB, and RFC, respectively. RFA, purified and shown to be deleterious to European corn-borer larvae (Beck and Stauffer, 1957), was subsequently identified as 6-methoxybenzoxazolinone, or MBOA (Loomis et al., 1957; Smissman et al., 1957). RFC was shown to be 2,4-dihydroxy-7-methoxy-1,4-benzoxazine-3-one, or DIMBOA (Beck, 1965). These early successes in isolating and identifying plant allelochemics with biological activities against insects led to significant improvements in the breeding of European corn-borer-resistant genetic lines of maize (Beck and Lilly, 1949; Beck, 1951; Beck, 1956b; Beck, 1956c; Beck, 1957a; Beck, 1957b; Beck and Stauffer, 1957; Beck et al., 1957; Loomis et al., 1957; Smissman and Beck, 1957; Smissman et al., 1957; Wahlroos and Virtanen, 1959; Beck, 1960; Beck and Smissman, 1960; Beck and Smissman, 1961; Smissman et al., 1961; Smissman et al., 1962; Bredenburg et al., 1962; Klun and Brindley, 1966; Klun et al., 1967; Klun and Robinson, 1969; Klun, 1970; Klun et al., 1970; Beck and Reese, 1976; Reese and Beck, 1976a; Reese and Beck, 1976b; Reese and Beck, 1976c; Reese and Beck, 1976d; Guthrie, 1979; Robinson et al., 1982a; Robinson et al., 1982b; Guthrie et al., 1986).

Stan Beck's studies over about 30 years reconciled the key elements of circadian rhythms and photoperiodic responses in insect seasonal time measurement and underscored the unifying principles of the biological clock. He stressed the necessary precision of insect timekeeping and showed that the biological clock regulates physiological processes without feedback that might interfere with its timekeeping function. His pioneering studies into the photoperiodic and thermoperiodic regulation of insect diapause induction and development, cold-hardiness, voltinism, and neuroendocrine regulation culminated in the publication of his dual-system theory of insect time measurement. Beck demonstrated that the integration of information about an insect's physiological, developmental, and behavioral systems, as well as its population ecology, is necessary to understand the temporal regulation and coordination of its life processes (Beck, Beck, 1968a; Beck, 1968b; Beck, 1983).

In the 1950s Stan Beck and his colleague, Jim Apple, were geographically well located in Wisconsin to study the voltinism of the European corn borer. The borer entered the United States around 1917 in Massachusetts and initially was univoltine. By the late 1930s a bivoltine population appeared in the east and north-central states. The ecotype with two generations per year reached Wisconsin around 1940. By the 1950s Beck and Apple were able to study geographical variation in the photoperiodic and temperature responses of this insect.

In 1961 Beck and Apple published a landmark paper on voltinism in the European corn borer in the *Journal of Economic Entomology* (Beck and Apple, 1961). They tested the hypothesis that the adaptation of the borer to particular local conditions involved changes in the frequencies of genetic factors controlling its photoperiodic responses. They plotted seasonal temperature accumulations against day length for three geographical populations of the corn borer in Illinois and Wisconsin and demonstrated that different geographical populations, exposed to different day lengths and temperatures, had different incidences of diapause. The practical significance of these findings provided the impetus for a North Central Regional Project (NC 20) to study geographical differences in the behavior and seasonal development of the European corn borer. This project is still active under a new number, NC 205.

Building on his early voltinism studies and continuing to use the European corn borer as his model insect, Stan Beck focused on gaining an increased understanding of the underlying mechanisms of insect seasonal time measurement. In his 1962 presentation at the twenty-third annual biology colloquium at Oregon State University in Corvallis, he commented: “The regular annual cycle of photoperiods forms the most precise basis known for the setting of the ‘physiological clocks’ by which biological events may be timed and synchronized. And, as might be expected, insects have taken full advantage of this possibility in their exploitation of evolutionary pathways” (Beck, 1963).

Stan Beck studied the interaction of day length and temperature on diapause induction and development. A photoperiodic response curve was obtained by plotting the incidence of diapause against the photoperiods under which European corn-borer larvae were reared. Diapause was induced only by a narrow range of photoperiods between 10 and 14 hours of light per day. The critical photoperiod (50-percent diapause) for a Wisconsin population of corn borers was between 15 and 15.5 hours of light per day. Subsequently, he expanded his photoperiodic studies to examine more closely the relationship between the light and dark phases in the daily photoperiod. The dark phase was shown to be the most effective in inducing diapause in the European corn borer (Beck and Hanec, 1960; Beck, 1962; Beck, 1988).

Stan Beck and his coworkers (Beck and Alexander, 1964; Beck et al., 1965) investigated whether a hormone produced by the proctodaeum of the European corn borer plays a role in diapause development. Beck named this hormone proctodone and concluded that the ileal epithelium is an endocrine center secreting proctodone in response to photoperiodic signals. In turn, the released proctodone was considered to control the activity of the cerebral neurosecretory system of diapause larvae. Beck used a two-oscillator model to explain the interaction between the secretion of proctodone and the secretion of prothoracicotropic hormone from the cerebral neurosecretory system. He postulated that an eight-hour subcircadian proctodone secretory rhythm is phase set by the onset of darkness, and that an eight-hour cerebral neurosecretory rhythm is phase set by the onset of illumination. Under long days the rhythms are in phase, but under short days the rhythms are out of phase. The conclusion was that proctodone activates the neurosecretory system under long days, when the two rhythms are in phase, but this does not occur under short days, when the two rhythms are out of phase (Beck, 1964).

The period from 1974 to 1985 can be called the integrative phase of Stan Beck's photoperiodic research. He developed a model to account for circadian and developmental photoperiodism (Beck, 1974a; Beck, 1974b; Beck, 1975; Beck, 1976; Beck, 1977; Beck, 1985). His dual-system theory of photoperiodic time measurement made the following assumptions:

- Different species share a common fundamental time-measuring mechanism.
- Photoperiodic determination of diapause or polymorphism involves gating in a manner identical to the gating of circadian rhythms.
- Two biochemical systems interact. Photoperiodic signals regulate the kinetics of these two systems: One system functions as a circadian pacemaker and as a determinative rhythm and the second system functions as a gating system.

Stan Beck developed this unifying theory when there were no corroborating molecular data to provide the underpinnings of the biological clock. It was an important stepping-stone to move the field forward.

Toward the end of his research career Stan Beck was convinced that interactions between day length and temperature cycles held the key to understanding how insect seasonal cycles are regulated. This quote from his 1983 *Annual Review of Entomology* article captures this point: "It is now becoming increasingly apparent that there are exceedingly significant biological responses to daily temperature cycles, with important interactions between photoperiodic and thermoperiodic adaptations. This promising facet of insect bionomics demands detailed investigation; it can no longer be ignored in our pursuit of the knowledge required to understand the fundamental characteristics of insect development and ecological strategies and to manage economically important insect populations."

SERVICE TO HIS PROFESSION AND REFLECTIONS ON HIS LIFE

Stan Beck was a member of the Entomological Society of America and served as its president and was a member of its Governing Board and Executive Committee, as well as other committees. He presented papers in national and international conferences and served on numerous task forces addressing ethical and disability issues. The society established in his honor the Stanley D. Beck Fellowship, a fund for disabled or disadvantaged students.

Those of us who shared Stan's professional life will never forget the sheer force of his will, determination, and intellect. He was paralyzed after contracting polio in 1952. In the ensuing decades he struggled valiantly against this disease. He ultimately was able to hold a pencil in one hand, to write, and could type with one finger. His hospital room looked like a college office with books and notes strewn all around the bed. The university loaned him a dictating machine to assist his efforts. Between therapy sessions and naps he continued to meet with graduate students and conduct other business. His mental processes remained unimpaired, and with his wide-ranging intellect he wrote and published classical scientific findings; books on scientific, theological, and fictional subjects; and countless articles for general scientific magazines. DeFoliart (2000) quoted Reginald H. Painter, the founder of the discipline of plant resistance to insects, as stating, "Ever since he [Beck] went back to his research [after being stricken with polio], with its outstanding contributions, I have considered that . . . he is one of the heroes of the human spirit. . . ."

One of us (J.C.R.) will never forget the day that Stan rolled out of his office announcing that he had just re-read a 1971 paper by Jim Truman and that he thought he had a new way of attacking insect photoperiodism. He immediately started to work on a mathematical model for the production and subsequent breakdown of two purely hypothetical substances. The math quickly outgrew his 128-step programmable calculator. He took a course in FORTRAN and was, we think, the first faculty member at the University of Wisconsin, Madison, to connect to the mainframe computer from his office. This work led to a series of publications on what he called the dual system theory (Beck, 1974a; Beck, 1974b; Beck, 1975; Beck, 1976; Beck, 1977), including another major review (Beck, 1983).

Stan also had a lifelong interest in the philosophy of science and devoted much effort to the communication of science to nonscientists (Chippendale and Reese, 1998). His first book *The Simplicity of Science* published in 1959 was nontechnical and written after he came home from the hospital. He believed that scientists should vigorously counter anti-science and anti-intellectual groups, which were becoming increasingly vocal in society (Chippendale and Reese, 1998). This concern for academic and scientific freedom was again manifested during his 1982 term as president of the Entomological Society of America. His presidential address, *Science and Politics* (Beck, 1983), addressed the problem of legislative and partisan political interference in science.

An anecdote provided by one of his former graduate students summarizes well how Stan conducted his career as a biologist with far-flung interests. He became interested in the phenomenon of retrogression, or the condition of certain species of beetle larvae getting smaller with each molt. In this project he weighed *Trogoderma* larvae and adults. He did this himself instead of asking his technician to do it, and in spite of his physical limitations. His explanation was that he needed a project of his own so that he would not "bug" his students too much about all the details of their projects. This indomitable spirit was summarized by Wallace Wikoff, writer for the Madison-published newspaper, *Wisconsin State Journal*, when he quoted Stan as follows: "Once you have adjusted yourself to the realization that you are—slightly incapacitated, then the road back is less difficult. For, sooner or later, you wake up to the realization that there are not many alternatives. You either must readjust your life or give up completely."

In an unpublished "Tribute to Stanley D. Beck" presented at the 1997 Entomological Society of America meetings in Nashville, Tennessee, Reese stated: "Dr. Beck used to talk about the bionomics of ideas and how a good idea or hypothesis may not last long, but will give rise to other ideas. In the same way, although he would probably like knowing that he is missed, it would please him far more to know that his contributions to his family, his science, and his professional society, have stimulated others to continue to make these kinds of contributions. These continuing contributions may be the greatest tribute we can pay to the memory of Stanley D. Beck."

IN CONCLUSION

We quote here from Chippendale and Reese (1998): "It is difficult to capture the multifaceted contributions of this remarkable scientist and man. For those who knew Dr. Beck, his legacy extends far beyond the written record of his accomplishments, his cutting edge research, and his exemplary teaching. He taught us a lot about life and how to persist in the face of seemingly insurmountable difficulties. In 1980 he wrote: 'Research may be characterized as the process of opening an infinite regression of black boxes.' He helped those around him to open their eyes to the full potential life has to offer. We were fortunate to be advised by Dr. Beck in our doctoral programs . . . and learned much of lasting value from observing his analytical approach to research problems, his skill in formulating hypotheses, designing and interpreting experiments, and from his philosophy of life."

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