BIOGRAPHICAL MEMOIRS

Bruce Wallace

May 18, 1920–January 12, 2015
Elected to the NAS, 1970

A Biographical Memoir by Stephen J. O'Brien, Ross J. MacIntyre, Lee B. Kass, Roberta S. Wallace, and James C. Fogleman

Figure 1 Bruce Wallace, April 1970. *Division of Rare and Manuscript Collections, Cornell University Library.*

Bruce Wallace made many extraordinary contributions throughout his career of more than seventy years in science and in society. A pioneer in population genetics theory and practice, he explored the concept of genetic load, first mentioned by Hermann Muller,[1] by designing and carrying out innovative experimental design and rhetorical descriptions of detail. Most of his research involved laboratory investigations using various species of Drosophila. He penned more than twenty books and monographs on subjects as diverse as adaptation, chromosomes, radiation, social biology, the environment, and gene action. His research extended the beauty and communication skills of his Ph.D. mentor, Theodosius Dobzhansky. His research publications and textbooks established him as a leader in the field of population genetics and as a gifted teacher. Importantly, he openly shared his ideas and deep understanding with his students and fellows at every level, as well as with collaborative professionals. His contributions were legend to evolutionary biologists and to the non-scientific public. In his later years, Bruce became prolific in social justice issues and biological ethics.

Early Life and Academia

Bruce Wallace was born on May 18, 1920, and raised in McKean, Pennsylvania, where he graduated from McKean High School. He attended Columbia University, and received his bachelor's degree in 1941. His future wife, Miriam, had graduated from Seton Hall College in Pennsylvania and was enrolled in a master's program at Columbia's Barnard College when they met; they were married in 1945. Bruce began his Ph.D. study under Theodosius Dobzhansky at Columbia in 1941, but his graduate studies were interrupted by World War II, and he enlisted in 1942. During the war, Bruce served as a statistical control officer under future U.S. Secretary of Defense Robert McNamara. After four years in the army, he returned to Columbia and completed his Ph.D. in 1949.

Prior to finishing his degree, Wallace was appointed as a research associate at the Department of Genetics, Carnegie Institution of Washington at Cold Spring Harbor (CIW/

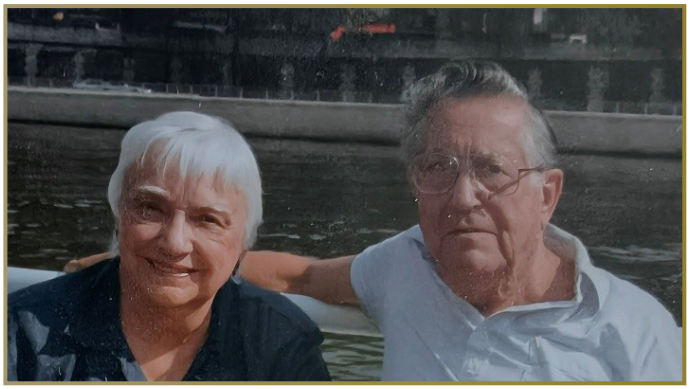

Figure 2 Miriam and Bruce Wallace (ca. 1980s). *Photo by Roberta S. Wallace.*

CSH) in 1947. From 1949 to 1958 he worked at the prestigious CSH Biological Laboratory of the Long Island Biological Association and served as the assistant director of the Biological Laboratory from 1954 to 1958. In 1958, he joined Cornell University as an associate Professor of Genetics in the Department of Plant Breeding and in 1961 was named Professor of Genetics. He later joined the newly established Section of Genetics, Development, and Physiology, Division of Biological Sciences, in 1965. During his tenure at Cornell, Miriam occasionally visited his lab to help out with stock maintenance. Bruce retired in 1981 to take a position in the Department of Biological Sciences at the Virginia Polytechnic Institute and State University in Blacksburg, Virginia. In 1983 he was honored as the University Distinguished Professor of Biology and was active until he retired in 1994.

Notable in his career was his early support for future Nobel laureate Barbara McClintock. While at the Biological Laboratory, Bruce attended the 1951 Cold Spring Harbor Symposium on Genes and Mutations, where she presented her research on chromosome organization and genetic expression. He had already learned firsthand about her pioneering discoveries and future Nobel Prize-winning research at the joint weekly meetings of the Biological Laboratory and the Department of Genetics. Years later, Bruce and one of his graduate students offered a model for understanding control regions of gene loci and how they might relate to mutable loci.[2,3] Bruce was instrumental in nominating McClintock as one of Cornell University's first Andrew Dickson White Professors-at-Large, commencing 1965.[4] Over the next nine years, she was hosted at Cornell by Bruce and his good friend and colleague, Cornell Professor Adrian Srb. McClintock's visits with Bruce, his students, and Cornell faculty had a lasting influence on their research.[5–8]

Scholarship and Scientific Influence

Bruce was a prolific and influential writer. He authored more than 160 peer-reviewed research articles, some twenty popular magazine pieces, and more than twenty published books. Of 180 science-based and popular articles, he was the first author for all but eight over a fifty-six-year period. His books on a wide breadth of subjects provide perhaps his greatest influence, and two books have become staples of college courses on population genetics across the world.[9,10]

It should be pointed out that although the field of population genetics was growing and improving during the twentieth century, the tsunami of influences and advances in molecular biology stimulated denigration by some. There were dissenting opinions by James Watson (CSHL), Francis Crick (Scripps Institute), and Gerald Fink (Massachusetts Institute of Technology) on the relative importance or relevance of population studies in a time dominated by molecular biology. Even Bruce's colleague, renowned population geneticist James Crow (University of Wisconsin), commented to potential graduate student Dan Hartl (later Higgins Professor of Biology at Harvard University) regarding the possibility of Dan joining Crow's lab: "Yes, Dan," Dr. Crow replied, "provided you understand that population genetics is a recondite field that will never be of great interest except to a small group of specialists."

The importance of the advances in population genetics since the 1960s are well known now in several applied genetics disciplines: genetic epidemiology, gene discovery, conservation genetics, and DNA forensics. Students trained by Hartl, Richard Lewontin, and Bruce would pioneer these applications in later years.[11]

Bruce wrote provocative, even prescient monographs on adaptation, genetic load, and gene action.[12–16] If not truly definitive, they were openly posing insightful scientific questions that were approached by scholars in later novel disciplines empowered by whole-genome sequence acquisition during the genomics era. For example, Bruce's research in quantifying genetic load, which advanced Muller's original concept to a higher level,[17] preceded an entire analysis discipline for species genome sequence analyses. The present field is developing better algorithms for assessing quantitatively the genetic load that wild species have accumulated over evolutionary time. Bruce mused and hypothesized on these features. Today, we discover them by genome mining. The same is also true for *The Search for the Gene* and *The Study of Gene Action.*[18,19]

Although his initial lab research focused on the subjects of genetic load, adaptation, and population fitness, Bruce's imagination led him to devise several unique ways to test specific theories. Among these are the "Artificial Crab," which was a laboratory test of Hampton Carson's observation of Drosophila larvae living among the bristles that were supplied by the excretory pores of certain tropical land crabs,[20] and the "Island Machine," which was used to test certain

Figure 3 Bruce Wallace and his daughter, Roberta, July 26, 2007, Cornell Plant Breeding Centennial. *Photo by Edward D. Cobb.*

Figure 4 Bruce Wallace with Ross MacIntyre and Stephen O'Brien, circa 2013. *Photo by Stephen O'Brien.*

assumptions of island biogeography.[21] These two novel and interesting examples illustrate Bruce's approach to important questions in population genetics, adaptation, and evolution.

Biology and Society: Ethical Contributions

Bruce was surely ahead of his time, offering compelling essays and books around societal concerns.[22–26] Bruce established a lecture series at Cornell in 1968 entitled "Science and Society," following the intellectual lead of E. O. Wilson and Stephen Jay Gould at Harvard. The faculty, students, and fellows were enraptured by the diverse and contemporaneous depth of content in the tumultuous times. His books and essays today make fascinating reading, and his papers can be accessed in the collections of the American Philosophical Society Library.[27]

Bruce's interest in environmental literacy prompted him to urge members of scientific societies to "… impress upon department heads, deans, provosts, and even college presidents their grave concerns" about populations and environmental problems and the lack of environmental literacy. He argued, "Only a sustained effort will focus the attention of college and university administrators (many of whom were themselves scientists) on the world's mounting population/societal/environmental problems … and will gain these problems the intellectual attention they deserve."[28]

During the Vietnam War, Bruce became active in the resistance movement as the country was torn apart by betrayed trust in government officials (including Robert MacNamara) about the rationale for invasion, extension, and justification of the huge death toll. His social conscience prompted him (along with Richard Lewontin) to resign from the National Academy of Sciences (NAS) in 1972, when they learned that the NAS, through its operating arm, the National Research Council, had staffed committees doing secret war research and funded by the Department of Defense. His resignation was considered a courageous act and one that exemplified his great strength of commitment to social justice. Only five other members had resigned from the National Academy of Sciences since the organization's founding in 1863. Happily, Bruce was reinstated by the NAS after the Vietnam War came to a close through the encouragement of NAS members, including his dear friend Mel Green.

Bruce left behind a legacy of successful students and fellows, including three authors of this memoir (RJM, SJO, and JCF). One of Bruce's postdocs, Ross MacIntyre, stayed on at Cornell and became a well-known and respected Drosophila geneticist. Bruce mentored eight Ph.D. students and several master's students at Cornell. They include Stephen O'Brien, James Fogleman, and John Gearhart. Gearhart is best known for first discovering and culturing human pluripotent stem cells.[29] O'Brien, an elected member of the NAS, contributed to developing the fields of genetic epidemiology, comparative genomics, and conservation genetics.[30] Fogleman has researched cytochrome P450 polymorphism in both Drosophila and humans and served as dean of the Division of Natural Sciences and Mathematics at the University of Denver.[31]

Honors and Awards

Bruce was celebrated with multiple professional honors and prestigious positions. He was elected a Fellow of the American Association for the Advancement of Science in 1955, and was elected to the National Academy of Sciences in 1970 and the American Academy of Arts and Sciences in 1971. He served as president of multiple scientific societies, including the American Society of Naturalists (1970), the Genetics Society of America (1974), the Society for the Study of Evolution (1974), and the American Genetics Association

(1990). Bruce was a co-editor of eight editions of Springer Link's Evolutionary Biology series and was heavily involved in the Biological Sciences Curriculum Study by BSCS Science Learning as a member of the executive committee. Bruce loved to travel and participated in many fellowships, lectureships, and visiting professorships, several of which were international. Bruce frequently traveled with Miriam and their children.

Bruce Wallace was a remarkable scientist, philosopher, and teacher. He allowed us to learn from him and, in essence, started us off on our careers in science. We, and his many students and colleagues both at Cornell and Virginia Tech, will never forget nor cease to appreciate this remarkable man. He died on January 12, 2015, in Blacksburg at the age of ninety-four. He was predeceased by his wife, Miriam, and is survived by his daughter, Roberta Wallace, of Wauwatosa, Wisconsin. His son, David B. Wallace, died on November 17, 2017.

Acknowledgments

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