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Obituary

Lindsay M. Black, 1907 to 1997

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Plant pathology and virology lost a pioneer when Lindsay MacLeod Black died on 23 December 1997. We lost a friend and mentor. Black was noted for proving conclusively that a plant virus can multiply in both leafhopper vectors and plants; characterizing unstable, leafhopper-transmitted viruses; and developing insect tissue cultures for studying plant viruses.

Lindsay Black was born in Edinburgh on 20 April 1907. The family emigrated to Saskatchewan, Canada, in 1914. With the aid of several scholarships, Black attended the University of British Columbia (UBC), Vancouver, to study plant pathology under F. Dickson and began a life-long friendship with C. Yarwood. Black received a BSA degree in 1929 and went to Cornell University, Ithaca, NY, to earn a Ph.D. in plant pathology under K. H. Fernow and F. M. Blodgett. He became a U.S. citizen in 1940.

As with many early plant virologists, Black started out working on potato viruses. He was intrigued by the viral diseases he saw when he inspected seed-potato fields as an undergraduate student. As a result, he switched his major from agronomy to plant pathology. Black researched potato yellow dwarf disease for his Ph.D. thesis and showed it to be caused by a virus (PYDV) transmitted by leafhoppers from nearby clover fields. After obtaining his degree, Black accepted a National Research Council Fellowship to continue research on leafhopper transmission of PYDV in L. O. Kunkel's laboratory at the Rockefeller Institute for Medical Research, Princeton, NJ.

Black discovered two new leafhopper-transmitted agents that cause wound tumor and clover club leaf diseases while searching for a new culture of PYDV. He assumed both were caused by viruses but eventually showed that clover club leaf is caused by a phytoplasma. He spent a major portion of his career studying PYDV, wound tumor virus (WTV), and clover club leaf.

The high probability of funding to study WTV, considered to cause "cancer" in plants, earned Black a position as curator of research at the Brooklyn Botanic Garden, NY, in 1946. In 1952, he moved to the Botany Department, University of Illinois, Urbana-Champaign, as professor of Plant Pathology, with a joint appointment in the Department of Plant Pathology, College of Agriculture. He stayed at the University of Illinois until his retirement in 1975.

Black's investigation of every aspect of WTV laid the foundation for future investigations on plant reoviruses. He studied the role of wounding in initiation of tumors, the morphology and histology of tumors, and new serological tests for assaying viruses and determining their location in hosts. The tumors produced were "immortal," i.e., they grew indefinitely in tissue culture, as do animal cancers. Black speculated that one of the main differences between plant tumors and animal cancers was the lack of metastasis in plants.

One of the burning questions concerning leafhopper-transmitted viruses during the 1950s was multiplication of viruses in leafhopper vectors. Black and others in Kunkel's group produced evidence of multiplication, but virologists from Europe and England vigorously disputed the idea, in part due to unfamiliarity, because no leafhopper-transmitted viruses had been found in Europe or England. Black spent several years proving conclusively that both the clover club leaf agent and WTV multiplied in leafhoppers and plants. WTV was the first virus shown to multiply in insects and plants.

A virus that multiplies in insects as well as in plants is as much an insect virus as a plant virus. Black and colleagues looked for the site of virus multiplication in insects and were the first to show the presence of a plant virus in thin sections of insect cells and organs. The ability of a leafhopper to vector a plant virus was shown to be genetically determined; different vector genes were effective for different viruses. Vector specificity among strains of a virus and loss of vector transmissibility in virus cultures maintained without vector transmission were reported, demonstrating the importance of virus genes for transmission.

Black was a pioneer in attempts to purify and characterize unstable insect-transmitted viruses. As a result, a versatile technique for purification of viruses and other particles, density-gradient centrifugation, was discovered in Black's laboratory. Previously, only small, stable viruses, such as tobacco mosaic, tomato bushy stunt, and southern bean mosaic, had been purified. Black and colleagues were the first to purify and visualize by electron microscopy a plant reovirus (WTV), rhabdovirus (PYDV), and tosposvirus (tomato spotted wilt).

Working in R. Markham's laboratory on an NIH Fellowship during 1961 to 1962, Black showed that WTV had a dsRNA genome. Subsequently, WTV was shown to contain 12 dsRNA segments, confirming WTV as the first known plant reovirus. Black and colleagues found that virus maintained in sweet clover by serially grafting from plant to plant for 20 years lost the ability to be transmitted by leafhoppers, although they continued to produce tumors in plants. Some "exvectorial" strains lacked any detectable amounts of segments 2 and 5, showing that these segments were not required for infection of plants or tumor formation but were candidates for genes for insect transmission.

Black realized that a better system for growing and assaying WTV was needed to investigate its molecular biology. He spent almost a decade successfully developing tissue culture methods for leafhopper cells for assaying and growing WTV. These methods facilitated resolution of many of the questions about the molecular biology of WTV.

Black was a dedicated and enthusiastic scientist, publishing his first paper (on a new potato disease) when he was an undergraduate student in 1929 and his last paper (on clover club leaf) in 1993. His research was carefully planned, with ample controls and replications. Black was a member of several professional societies and was active in professional affairs. To further communication among virologists, Black, with Luria and Hirst, started the journal *Virology* in 1955. Black was the first editor for plant viruses, a duty he performed ably until 1965. He became a Fellow of the American Phytopathological Society in 1966 and received the Ruth Allen Award in 1978.

Lindsay Black's research achievements were important, but his teaching and mentoring were equally important. He taught general plant pathology at the University of Illinois for more than 20 years and supervised many graduate students and post-doctoral fellows. He was modest, kind hearted, and fair, treating every individual who worked with him equally and attracting students and post-doctoral fellows from every continent. The guidance provided by Black, the opportunities he provided to investigate challenging problems, and the continued support he so generously gave helped many of his students to build successful careers in virology.

Lindsay married Helen Wilhelm, a high school teacher and botanist, in 1936. She supported Lindsay in his career and graciously welcomed his students and associates into their home. Both Helen and Lindsay read widely and were avid naturalists. A walk with Lindsay, in his backyard or in a national park, was an education in biology, from interesting trivia to broad principles. All of Blacks' students have fond memories of the time they spent in his laboratory.

Lindsay is survived by his wife Helen, his son Dr. Lindsay W. Black, his daughter Anne Mangel, and two grandchildren. He was preceded in death by his son Dr. Douglas Black.

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