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JOSEPH MICHAEL DALY

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A Biographical Memoir by
MYRON K. BRAKKE

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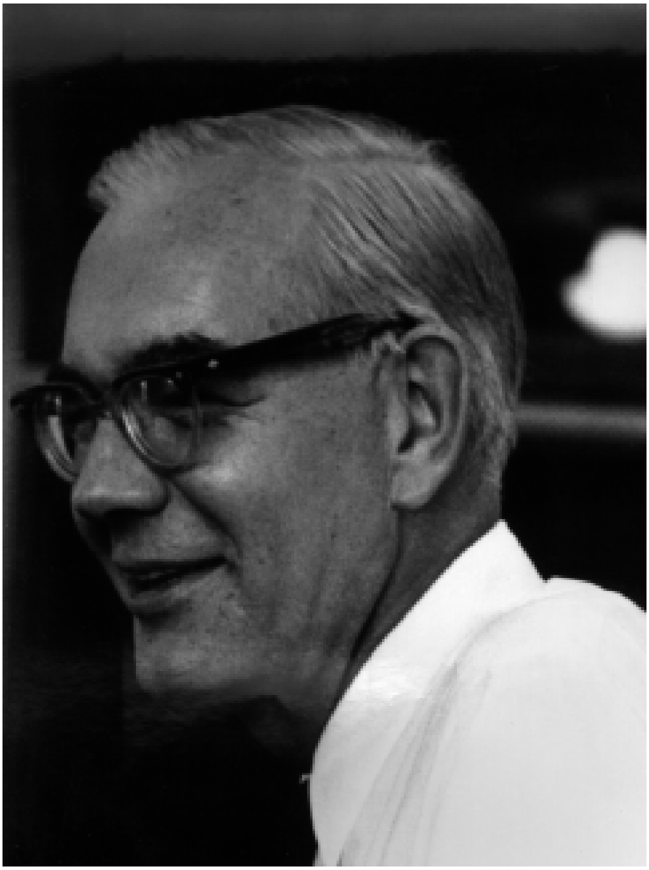

J. M. Daly

JOSEPH MICHAEL DALY

April 9, 1922–August 18, 1993

BY MYRON K. BRAKKE

JOSEPH MICHAEL (MIKE) DALY was an expert on the physiological interactions of plants and their fungal pathogens. Most of his research was on the rusts of wheat and bean, but he also investigated toxins produced by *Helminthosporium* species.

Research on rusts was difficult because the fungi could not be grown independent of the plant. Physiological differences between healthy and rusted plants reflected the metabolism of the rust fungus itself and changes in the plant's metabolism caused by the rust. Attempts to separate the two effects gave numerous theories and led to spirited discussions in which Daly reveled and excelled. His abilities to discover logical flaws in facile theories made him a respected leader in his field.

In the last part of his career, Daly turned to another system—the plant diseases caused by fungi that produce toxins. Daly purified and determined the structure of the toxin of the fungus that caused the devastating southern corn leaf blight epiphytotic of 1970 and participated to varying degrees in studies of other similar toxins.

PERSONAL HISTORY

Joseph Michael Daly was born in Hoboken, New Jersey, to Julia (nee Yarwood) and Michael Daly on April 9, 1922, and grew up in Newport, Rhode Island. His father died when he was young, leaving support of the family to his mother. Daly spoke of her often and of how hard she worked in unskilled jobs to support the family. Daly was always Joe or Joseph to his mother, but there were too many "Joes" in plant pathology at the University of Minnesota, so Daly was always known as "Mike" to his fellow scientists.

Although he wanted to work to help support the family after high school, Daly's mother strongly encouraged him to go to college. He worked his way through Rhode Island College, where he was influenced by botanist Vernon Cheadle and plant pathologist Frank Howard to pursue a career in plant pathology. After obtaining his B.S. degree, Daly went to the University of Minnesota for graduate studies in plant pathology. There he married Cecilia Rieger, a botanist with an M.S. from Vassar. They had six daughters and two sons, all of whom survive: Katherine O'Rourke, Anne Schmidt, Melissa Hoy; Martha, Cecilia, Constance, Stephen, and Timothy Daly.

Family and religion were important parts of Daly's life. He served on the Catholic Social Service Board and was involved in educational efforts to promote awareness of the sanctity of life. At home he led the family's lively dinner-hour discussions and strongly encouraged his children in their diverse interests. He was proud of his wife when she obtained her second M.S. degree, in computer science, after raising eight children. She taught computer science and counseled students for many years at the University of Nebraska.

I first knew Mike Daly when we were both graduate students at the University of Minnesota, he in plant pathology and I in biochemistry. Later, his recommendation helped me obtain a position with the U.S. Department of Agriculture in the plant pathology department at the University of Nebraska to start an association that lasted more than thirty years. Although we worked on different diseases of plants, it was a small department and I knew his students and his research problems as he knew mine. We shared equipment and for a while even an 8 × 12 foot office.

Mike was an intense and enthusiastic scientist, critical of his own work and that of others. Throughout his career he spent time at the laboratory bench doing crucial experiments himself. He checked and double checked his own experiments before drawing conclusions and often double checked those of others as well. He checked the calculations on most of the papers he refereed. His criticisms, both written and vocal in meetings and informal gatherings, set the standard for the field. Nobody got away with a bad conclusion as long as Mike was around.

Mike loved camaraderie and a good story. He was vastly amused by the foibles of his fellow man. One of Daly's favorite stories was of a fellow graduate student at Minnesota, who won and kept a dime from a bet on a rebroadcast of a prize fight that he had heard before. An enthusiastic sportsman and a gardener, Mike was an avid golfer with an incurable slice and a fervent fan of the Celtics basketball team and of Notre Dame football. He told me that Notre Dame players, some of whom he had had in class, were real gentlemen, not the jocks found at lesser schools!

GRADUATE EDUCATION

The plant pathology department at Minnesota was dominated by its head, Dr. Elvin Stakman, an NAS member. Stakman had formulated the concept of physiological races of rust fungi to explain the variations in the patterns of disease severity caused by fungi from different sources when tested on a selection of cultivars of wheat. The susceptibility of a cultivar depended on the source of the rust fungus used to inoculate it and vice versa; the severity of the disease depended on the wheat cultivar on which it was tested. The rust pathogens from different sources were identical morphologically, and, therefore, their virulence differences were attributed to physiological differences, and they were termed "physiological races."

Many of the graduate students at Minnesota investigated some aspect of the physiology of plant disease. Physiology at the time included nutrition and environmental effects. Daly obtained an M.S. degree in 1947 under Helen Hart, after thesis research on the influence of nitrogen levels in the soil on the development of stem rust of wheat.

Daly next wanted to use biochemical methods to study the basis for the physiological differences of the rust races. To do so, he left the plant pathology department for the botany department at the University of Minnesota, but he did not leave his interest in plant diseases.

In changing departments Daly showed that he thought for himself, a characteristic that would make him a leader. I doubt that Stakman liked his departure. Stakman was a dominant figure in plant pathology, not only at Minnesota but nationally, and was deeply interested and involved in the training of graduate students and their subsequent careers. He did not like to lose good graduate students. Daly was an excellent student, willing to do the extra jobs that kept the department functioning. For example, he produced the index for 1946 through 1949 for the journal *Phytopathology*, which was edited by Helen Hart.

Daly's relations with Stakman were a bit strained until they had a cordial conversation at a meeting of the American Phytopathological Society in the late 1960s. Daly felt he was forgiven.

PROFESSIONAL HISTORY

Daly completed his Ph.D. degree in 1952 under Dr. A. H. Brown in the botany department at Minnesota with a thesis on the presence of cytochrome oxidase in the leaves of higher plants and became one of the early users of mass spectrometry for physiological investigations. Upon graduation he accepted a position at the University of Notre Dame to teach botany. In 1955 Dr. Bill Allington offered him a position in the plant pathology department at the University of Nebraska with freedom to start his own research program. Daly accepted and started a research program on the physiology of rusted plants.

Daly was a professor of plant pathology at the University of Nebraska until 1964, when he moved to the Department of Biochemistry and Nutrition as professor of biochemistry. In 1966 he was named C. Petrus Peterson Professor of Biochemistry at the University of Nebraska, a position he held until he retired.

Daly was primarily a teacher and researcher, but he also was an able, though reluctant, administrator. From 1962 to 1964 he was chairman of the Department of Plant Pathology at the University of Nebraska. He provided leadership to the newly formed School of Life Sciences during 1973-74 as its first director.

Daly's advice was highly valued, and he was asked to serve on numerous committees and panels of university, government, and professional societies. He was an influential teacher through the courses he gave and the students and postdoctoral fellows he trained in his laboratory. He believed in close personal supervision of students and to that end had only a few students in his laboratory at any one time.

Daly received many honors and gave numerous invited seminars and symposium talks, wrote many book chapters, and edited books and journals. He was elected to the National Academy of Sciences in 1984 and to the American Academy of Arts and Sciences in 1986. His publications reveal collaborations with scientists at several institutions, in addition to students and postdoctoral fellows. His most frequent collaborator was Herman Knoche, a fellow professor in the biochemistry department. Daly had close ties with Japanese scientists, particularly I. Uritani, Yoshiki Kono, and Yoshikatsu Suzuki. He was an active participant in a series of cooperative science seminars on the physiology of plant disease jointly sponsored by the National Science Foundation of the United States and the Japan Society for the Promotion of Science. Daly coorganized a seminar titled "Recognition and Specificity on Host-Parasite Interactions" held at the University of Nebraska in 1977. The last of these seminars that he attended, in Nagoya, Japan, in 1985, especially honored him.

RESEARCH

Rusts have been important diseases, often limiting humans' food supply, since the beginning of agriculture. As obligate parasites, rust fungi obtain their nutrients and energy from host plants. The contribution of the rust fungus to the host plant is less clear, although the formation of pustules containing spores is an obvious morphological disruption of plant tissue. Some rust-infected plants produce galls, which are part plant and part fungal tissue, suggesting a growth-controlling effect of the fungus on the host. The narrow host range of the fungus and the presence of physiological races of the fungus show that subtle differences, under genetic control in both host and fungus, can determine whether disease develops.

The above brief facts were known when Daly started his research. Daly and others tried to understand the interaction of fungus and host, partly out of curiosity and partly to help devise logical ways to control diseases. One aspect Daly investigated was the energy and nutrient supply to the fungus; another was specificity or the mutual recognition between pathogen and host that determined if the disease would develop; a third was growth stimulation of the host caused by the rust.

The hallmark of Daly's investigations was thoroughness. He investigated the respiration of rusted tissues at all stages of rust development, in near-isogenic lines differing in a gene for resistance, in lines with temperature-sensitive resistance genes, and with many approaches—inhibitors, labeled precursors, kinetic studies, anaerobic versus aerobic conditions, and others. Theories postulated by others and supported by data from a limited set of conditions often were unsupportable when tested under such a variety of conditions.

Daly produced strong evidence that the fungal tissue itself contributed to respiration of the host-parasite complex, particularly at sporulation. Furthermore, rusted leaves and hypocotyls were metabolic sinks into which sugars, sugar alcohols, and other metabolites were transported from uninfected parts of the plant. The rusted tissues not only needed extra nutrients for growth of fungal mycelium and spores, but the rusted bean leaves and safflower hypocotyls were often larger than comparable healthy tissue.

Some investigations showed that rusted tissue had high concentrations of indoleacetic acid (IAA), a growth-regulating hormone, a plausible explanation for the increased respiration and growth. However, it was hard to obtain consistent results in IAA assays because of technical difficulties in assaying leaves for hormones without interference from contaminating microbes. Daly investigated the metabolism of IAA in leaves and found that resistant inoculated tissues had higher levels of peroxidases and IAA decarboxylases than uninfected or susceptible rusted tissue. However, high levels of peroxidase persisted in the presence of ethylene or high temperature, both of which broke the resistance and allowed development of spore pustules. The hypothesis that high levels of peroxidase caused resistance was untenable.

In postulating reasons for the difference between resistant and susceptible cultivars, most plant pathologists consider susceptibility the norm and resistance to be an active mechanism induced by the presence of the pathogen. However, most fungi do not cause disease in most plants. The common viewpoint is to say that this is "nonhost" resistance, operating by a mechanism separate from that responsible for resistant and susceptible cultivars of a single species. Daly suggested that resistance was the norm and that susceptibility was induced by the right combination of pathogen and host. He argued that all observations, including that of Harold Flor's on flax rust, which led to Flor's gene-for-gene hypothesis, could be explained by the induced susceptibility hypothesis.

PATHOTOXINS

Widespread infection of corn with *Cochliobolus heterostrophus (Helminthosporium maydis)* race T in the United States in 1970 caused the loss of about 15 percent of the corn crop. Race T was rare in the United States before this, although it occurred elsewhere and race O was common in the United States. Maize geneticists soon showed that *H. maydis* race T devastated maize with Texas male-sterile cytoplasm, which was widely used to save the labor of detasseling in growing hybrid seed corn.

It was soon found that culture filtrates of *H. maydis* (which is not an obligate parasite) caused typical disease lesions on T-cytoplasm corn but not on N-(normal) cytoplasm corn. This result showed that a fungal toxin caused the symptoms and that the specificity between T- and N-corn was due to the toxin. If the toxin could be purified, it would simplify the study of genetic specificity. Daly undertook the purification and characterization of the toxin with the help of several collaborators. In addition to being project leader, he got his hands dirty, literally, purifying the toxin with charcoal and chromatography. Toxin he purified has been sent to scientists worldwide for investigations on toxin action.

As a preliminary step to purification of the toxin, Daly sought a better bioassay than root growth inhibition. The toxin inhibited both photosynthesis and dark CO_2 fixation. Daly showed that an assay based on dark CO_2 fixation was quicker, more reproducible, and more accurate than assays based on root growth inhibition or ion leakage.

Purified toxin was needed for investigating mechanisms of action, and Daly concentrated on purifying the *H. maydis* toxin and determining its structure. He and his colleagues were soon successful and reported the toxin to be a family of long-chain, linear, saturated hydrocarbons with odd numbers of carbon atoms and four clusters of oxy/oxo groups. The three main constituents were $C_{42}H_{68}O_{13}$, $C_{39}H_{66}O_{12}$, and $C_{41}H_{70}O_{13}$. The oxy/oxo clusters were mixtures of 3, 5-dihydroxy ketone, and 3-hydroxy, 5-keto ketone sequences. The clusters were separated by three or five methylene groups.

Biochemist Herman Knoche gave major help in purifying the toxin, and organic chemist Yoshiki Kono assisted significantly in determining the structures during a two-year stay at Daly's lab. Kono continued to collaborate with Daly after he returned to Japan.

Daly and Yoshikatsu Suzuki synthesized the stereoisomeric

C_{41} compound and showed it to be as toxic as the natural toxin. The synthetic C_{23} analog, with three methylene groups between two oxy/oxo clusters, was only slightly less toxic than the C_{25} synthetic analog with five intervening methylenes, but both were 300 times less toxic than the natural toxin. All the synthetic compounds had the same specificity toward corn as the natural toxin; that is, they were toxic to T-cytoplasm corn but not to N-cytoplasm corn.

The C_{24} synthetic analog with four intervening methylenes was slightly less toxic than the C_{25} analog, but the C_{26} analog with six intervening methylene groups was less than one-tenth as toxic as the C_{25} analog, showing the importance of the length of the intervening methylene groups between the clusters of oxy/oxo groups.

H. maydis is not the only pathogen to cause a disease specific to corn with T-cytoplasm. An unrelated fungus, *Phyllosticta maydis,* causes a leaf blight of corn with T-cytoplasm. Daly and colleagues purified the toxin of *P. maydis* and showed it to be a mixture of linear hydrocarbons, $C_{33}H_{60}O_8$, $C_{33}H_{62}O_8$, $C_{35}H_{66}O_9$, and $C_{33}H_{62}O_9$. As with *H. maydis* T-toxin, the PM toxin has four clusters of oxo/oxy groups separated by three or five methylene groups. However, the PM-toxin mostly has only two oxo/oxy groups per cluster rather than the three of *H. maydis* T-toxin. Purified PM-toxin and synthetic toxin were equally effective on mitochondrial oxidation in vitro and on dark CO_2 fixation by leaf slices. Both were a few times more active on a molar basis than the *H. maydis* T-toxin.

Daly also collaborated with Larry D. Dunkle in determining the structure of the host-selective toxins of *H. carbonum* and with V. Macko in determining the structure of the *H. victoriae* toxin.

Determining the structure of the toxins and synthesizing analogs was only the first step in Daly's planned investigations of the host-selective toxins. He wanted to use the toxins as tools to investigate the physiological basis for the host-parasite specificity. He started this investigation by studying the effect of T-toxin on dark CO_2 fixation, photosynthesis, and mitochondrial oxidation of NADH, succinate, and malate. His research was cut short by an untimely stroke in 1986, only two years after he was elected to the National Academy of Sciences. His contributions continued after his stroke, as his stocks of purified toxin were distributed to colleagues for investigations of action, including the identification of mutations in mitochondrial genes of T-cytoplasm corn.

CONCLUSION

One of Daly's lasting contributions was the rigorous standards he brought to physiological investigations of plant disease. Physiology of pathogenesis was emerging when Daly became active, and he contributed more than anyone else to the establishment of high investigative standards. His critical analyses were crucial in a field where conclusive experimental evidence was difficult to obtain.

Another of Daly's main contributions was the purification, structure determination, and synthesis of the host-selective phytotoxins produced by *Helminthosporium* and other fungi. He set the stage for application of the molecular techniques that subsequently became available. But Daly's most lasting contribution may be the students and postdoctoral fellows he trained and influenced. He was an enthusiastic teacher who challenged his students with penetrating questions that stimulated thinking and lively discussions. Students who took his courses frequently came to him throughout their graduate careers for advice on research problems and professional matters. His greatest professional satisfaction came from letters written by former students who told him how much they appreciated his efforts in creating an environment for learning, to get them to critically read scientific literature, and to be equally critical of their own work.

I AM INDEBTED TO Mrs. Cecilia Daly for information on Mike's early history and personal life. Herman Knoche, Larry Dunkle, and M. G. Boosalis provided personal and professional information on Mike. Secretaries at the biochemistry department of the University of Nebraska kindly made their files available.

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