Richard R. Nelson, 1926–1991

R. D. Schein, Scot C. Nelson, and J. F. Tammen

Department of Plant Pathology Contribution 1968.
We are thankful for the assistance of H. Cole, Jr., K. J. Leonard, D. R. MacKenzie, W. L. Pedersen, R. K. Webster, and R. D. Wilcoxson, all close colleagues of R. R. Nelson, who were especially helpful in commenting on his research contributions.

Richard R. Nelson of The Pennsylvania State University, University Park, died 28 April 1991, at his home in Naples, FL, after a long illness. He had retired in 1985. For 30 yr, from 1955 to 1985, he was one of our profession's most original and productive members.

Nelson was born in Austin, MN, on 23 May 1926. He received a Bachelor's degree from Augsburg College, Minneapolis, MN. He completed his Master's and Doctoral degrees in Plant Pathology with minors in Plant Breeding and Genetics. From 1953 to 1955, after his doctoral studies, Nelson served as a Rockefeller Foundation Research Fellow in Plant Pathology at the University of Minnesota, St. Paul. In 1955, he joined the USDA Crops Research Branch, as plant pathologist and was assigned to North Carolina State University, Raleigh, where he also held an adjunct appointment to the faculty in Plant Pathology. In 1966, he was appointed Professor of Plant Pathology at The Pennsylvania State University, and in recognition of the truly significant contributions he was making to graduate study and to research, in 1974 he was appointed Evan Pugh Professor of Plant Pathology, the university's highest rank.

Dick's research, published in over 270 papers, surprising in scope, forms a definitive, comprehensive, and altogether distinguished body of work. It contains an easily discernible scientific continuity that began in 1953, just as Dick completed his doctoral studies. Under E. C. Stakman and J. J. Christensen and funded by The Rockefeller Foundation, he began a study which his associate Roy Wilcoxson described as monumental: "to make pathogens more virulent and hosts more resistant." The pathosystem was *Puccinia graminis* f. sp. *tritici* and wheat.

The approach was to prepare mixtures of races, to inoculate wheat rust "differentials," and to test and retest for "accumulated" genes for virulence. This is a distinct foreshadowing of his last works on gene pyramids. Typical of Nelson, thousands of mixtures were prepared and tested until, finally, a race occurred that attacked the most resistant differential, Khapli. Continued inoculations and reinoculations with the progeny of this race resulted in the occurrence of types nonpathogenic to Khapli. He thought these results could be explained by the association and disassociation of nuclei in somatic heterocaryotic hyphae. Histologic and marker gene studies revealed that, indeed, nuclei occur in hyphal cells of *Pgt* in numbers greater than two.

The impact of this original, landmark research was at least twofold: Dick was among the first in our science to discover that heterocaryosis played a role in the pathogenicity and virulence of fungi and that new races of wheat rust could arise from what we now term somatic recombination. This early experience set Dick on a course that lasted a lifetime: the interrelated genetics of pathogenicity and host resistance, studies which, by plan and serendipity, have had and will continue to have a major impact on our science and on world agriculture.

The second phase of Dick Nelson's career began in 1955 and lasted until 1966, during which time he was a pathologist in the Crops Research Division, USDA, and adjunct professor of Plant Pathology at North Carolina State University. He was responsible for studies of *Helminthosporium* diseases of corn. He proceeded with the same thoroughness and technique he used at the University of Minnesota to unravel the relationships among the various host-delimited graminicolous species of *Helminthosporium*. Recognizing that the "species" of *Helminthosporium* were spurious, based as they were on morphology and host rather than other biology, including the sexual stage, he collected, cataloged, and stored every *Helminthosporium* from leaf spots on gramineous hosts, cultivated and wild, that he could gather from around the world. His factorial studies testing hundreds of isolates against a selected range of gramineous hosts showed clearly that the classification of the species, based on asexual spore morphology and host, had little value. Morphologically different "species" attacked the same hosts; host specificity was more often the exception than the rule. It appeared obvious to him that the classification scheme for *Helminthosporium* required major revision based on biological relationships if pathogenicity in and resistance to the fungi in this group was to be understood.

Thus, Dick concurrently initiated intensive studies on the genetics of sexuality as it related to taxonomy and to pathogen-suscept relationships. These studies, following those of Drechsler (1925, 1934) and Tinline (1951) began with Dick's discovery that *Helminthosporium maydis* is heterothallic and that the perfect stage, *Cochliobolus heterostrophus*, can be readily produced in the laboratory if the appropriate mating types are used. With this knowledge, Dick undertook comprehensive studies of the genetics of sex and, with his associates, on the genetics of pathogenicity and resistance, which have had and will continue to have a major impact on our science and on world agriculture. Over 30 papers on the genetics of sex and more than 20 papers on the genetics of pathogenicity in *Cochliobolus* and *Helminthosporium*, many with his friend and colleague David M. Kline, were published during this second phase. A similar and equally important work was carried out with *Trichometasphaeria turcica*. In this same period, he conducted studies with W. E. Rogers on the biology and pathogenicity of witchweed, *Striga asiatica*, with Frank H. Nassis and D. M. Marx on the genetics of sex and pathogenicity of *Phytophthora*, and with D. Huisingh and R. K. Webster on the role of sterole biosynthesis in sexual differentiation in *Cochliobolus*.

Dick Nelson was a genius, with a gift for conceptualizing, designing, and conducting research that would provide not only specific answers to specific questions, but that would contribute to our understanding of broader biological phenomena. Clear evidence of this is his conceptualization of the "biological species," as opposed to the "practical" species. His concept of the "biological species" and the strong body of evidence he built in support of it have played a key role in the classification of *Helminthosporium* and related genera. His work on the genetics and evolution of sex and pathogenicity and on pathogenicity and resistance, conducted with Dave Kline, and later with Alice L. Robert and G. F. Sprague, forms another striking example.

The third and last phase of Dick Nelson's career began in 1966 at Penn State as professor of Plant Pathology. At a little over 40 yr of age, he was ready for new scientific adventures, and the results were spectacular. He was enticed to go to Penn State for at least two reasons: The department there was recently established, and the faculty was committed to strengthening its programs of graduate study and quantitative epidemiology, two areas in which Dick was intensely interested and to which he felt he was prepared to make major contributions—indeed he did.

Nelson's intricate understanding of the *Helminthosporium-Cochliobolus* pathosystem was used as the basis for work on the nature of complementary host resistance and pathogen virulence. Starting in the mid-1960s, he developed ideas about the bases of vertical and horizontal resistance. He advocated gene-deployment strategies, including multilines, to provide stability to major gene-resistance systems. In the 1970s, he moved to a consideration of additive effects of resistance-gene dosage. Observing "tag-along" effects that sometimes affected the rate of disease development, he began to visualize that these effects might be caused by linkage groups or "minor" genes associated with major genes. Dissatisfied with the qualitative term "aggressiveness" to characterize the strength of disease induction by pathogens, with its implication of superior survival by the most aggressive, a concept that failed to consider that natural pathosystems do not inevitably evolve toward greater disease severity, he formed an idea about the nature of stabilizing selection quite different from that of Vanderplank. Nelson recognized that a pathogen's ability to survive and thrive in the field does not necessarily correlate exactly with the severity of the disease it induces. In this context, the idea of relative parasitic fitness became important, and methods of quantifying it resulted. Nelson also developed the concept that the defeated gene for resistance had a possibly important rate-reducing effect; accumulation of these could achieve stability in pathosystems. This differed from Vanderplank's view that the defeated resistance gene was superfluous, an attribute that could lead to its loss from the pathosystem.

Omitted here are the names of the various students, colleagues at Penn State, post-doctoral associates, and colleagues at other universities and research organizations who responded to Nelson's stimuli, producing lab and field work as well as further theoretical models and extrapolations. The ideas, with further modification, are the basis of current research and strategy development in disease management. Defeated gene pyramiding has not been fully tested, having paused in the early 1980s because of serious problems in building a large enough, properly understood, pyramid that allows definitive testing. Recombinant DNA research may eventually provide further elucidation of this advanced idea originally postulated by Nelson.

At Penn State, besides being preceptor for a number of graduate students, Nelson taught several courses at one time or other but was particularly committed to a discussion course for doctoral candidates approaching the end of their studies. In this course, he stimulated serious intellectual discussion and caused students to defend or attack ideas he put forward for discussion. No student went through this experience without being seriously intellectually challenged. Dick knew he was using the method of Socrates. He considered himself to be a Stakman protégé, and learned the technique at Stakman's knee. He admired E. C. Stakman above all other plant pathologists. Besides teaching, he served the department, the college, and the university on many important committees. His years as chairman of the department graduate studies committee were particularly productive.

His strength did not go unrewarded. He was made a Fellow of the Society in 1971 and was given Penn State's highest rank of Evan Pugh Professor in 1974. He was a distinguished visiting lecturer at the University of California, Davis, in 1981 and at the University of Barquisemeto, Peru, in 1983. He was a distinguished visiting scholar at the University of Hawaii in 1973. His research was sponsored by USDA-CSRS, NSF, NIH, and the Rockefeller Foundation, and by Pioneer Seed Company and the Penn Crop Improvement Association. Professional travel took him to all parts of the country and to Europe and Latin America to give special seminars or to participate in research conferences. It was natural that he played a large role as a strategist in the preparation for the battle against southern corn leaf blight in 1971. Besides his journal publications, he was the editor and a contributing author to *Breeding Plants for Disease Resistance—Concepts and Controversies*, which was dedicated to his colleague C. C. Wernham who initiated the effort but died before it could be completed.

He served the American Phytopathological Society as a member of the advisory board to the American Type Culture Collection and on the committees for genetics and host resistance, mycology (chairman), epidemiology (chairman), plant disease management (chairman), corn compendium, and national corn disease monitoring. He was a member of the editorial committee of the *Annual Review of Phytopathology*.

When one who knew Dick Nelson well reviews his curriculum vitae and, particularly, his chronologic publication list, one is struck by the fact that this man, so original in thought, a man who seemed to cultivate his reputation as an iconoclast, published more often than not with his many students and professional colleagues, on a wide range of subjects. There are several-year-long series of very important papers coauthored with D. M. Kline, R. K. Webster, J. E. Ayers, and D. R. MacKenzie. There are dozens of papers in the list of 270 he contributed in which one finds the names of those who have gone on to produce high-quality work in important positions at home and abroad.

To work with him was extremely intellectually stimulating. He was a man of few words and probing questions. Superficiality of thought never went unremarked. Yet, he championed many a student who was struggling. Only Dick Nelson's closest friends knew bits and pieces of his early years. His childhood was extremely difficult, with very serious familial and economic problems. His obvious intellectual capacity linked to dogged persistence got him to college and that carried him to a first job as a high school coach. It was while earning extra summer credits that he came to the attention of E. C. Stakman, who not only recognized Dick's special intelligence, but induced him to switch to plant pathology, found him support, and gave our field another of his famous students.

Dick Nelson was an original—there was never one like him before and there will not be another like him again. One of his closest colleagues remarked that "Dick never met an argument that he didn't like!"

Dick was married in 1947 to Sally Hicks, who survives. They had four children: Richard, Scot [a plant pathologist], Shelley, and Mark, and three grandchildren. A memorial fund was established by his family in support of graduate education in the department at The Pennsylvania State University, which welcomes contributions.