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Review

Finding our roots and celebrating our shoots: Plant virology in *Virology*, 1955–1964

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ABSTRACT

To celebrate the sixtieth anniversary of *Virology* a survey is made of the plant viruses, virologists and their institutions, and tools and technology described in the first decade of plant virus publications in *Virology*. This was a period when plant viruses increasingly became tools of discovery as epistemic objects and plant virology became a discipline discrete from plant pathology and other life sciences.

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Introduction

In May 1955, the inaugural issue of *Virology* was published under the editorial direction of three eminent virologists at the University of Illinois-Urbana—George K. Hirst, Lindsay M. Black, and Salvador E. Luria—to "further communication among virologists" (Brakke and Reddy, 1999). They divided their editorial duties by areas of expertise with Hirst, the editor-in-chief, taking manuscripts on animal viruses; Luria the bacterial viruses; and Black the plant viruses. The establishment of *Virology* suggests the discipline had matured sufficiently to support a specialist journal. In 1953, in his textbook "General Virology", Luria wrote that "virology should be concerned primarily with virus functions and properties", a prescription closely followed by the founders of *Virology*.

The mid-20th century was an auspicious time to begin a new journal, in part due to two key events in the 1950s that greatly

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influenced scientific advances in the United States, a decade after World War II. The first event was the establishment of the National Science Foundation (NSF) in 1950, and disbursement of research grants in 1952. The second event was the launch of Sputnik-I by the USSR on 4 October 1957, ushering in a push for Cold War-scientific advances and increased funding for research and development. (As an aside, Sputnik launched the same day that Robert Horne and Sydney Brenner first observed T2 phage using phosphotungstic acid as negative stain (Horne, 1999)).

The history of bacteriophage and animal virology in this period is often discussed and celebrated by virologists, but less attention has been paid to advances in plant virology in the mid-20th century. The focus here is to use *Virology* from 1955 to 1964 to make some generalizations about plant virology and how the science was developed by a select group of research centers and scientists. With the focus on *Virology*, and space limitations, there will be only limited contextualization of scientists, institutes and viruses that fall outside these narrowly defined parameters. To celebrate sixty years of *Virology*, the favored viruses, techniques and equipment that advanced the field are discussed, with a particular emphasis on the top five plant virus papers based on peer-citations.

Which virus to study?

In the first decade of *Virology* plant virologists favored *Tobacco mosaic virus* (TMV). This reflected several decades of research, predicated on the finding of Martinus W. Beijerinck in 1898, when he reported that the mosaic disease of tobacco was a *contagium vivum fluidium*—a virus (Beijerinck, 1898 [1968]; Zaitlin, 1998). TMV was studied because it was important to tobacco growers, with significant agricultural losses reported in Europe and the United States (Scholthof, 2004). TMV, of course, was not the only virus associated with crop losses that became a laboratory object. Several potato viruses causing significant losses in the field, including *Potato virus X* (PVX), *Potato virus Y* (PVY), and *Potato yellow dwarf virus* (PYDV), were making their way into the research laboratory for physicochemical study.

Turnip yellow mosaic virus (TYMV) is a particularly intriguing example of how an economically important virus travels from the field to the laboratory and becomes an epistemic object. Until preparing this essay, it was unclear to me why TYMV was a favored laboratory virus in the mid- to late-20th century. As with TMV and potato viruses, the scientific roots of TYMV can be found in the field. In 1944 Kenneth M. Smith, a plant pathologist at the Plant Virus Station at Cambridge (UK), and his Ph.D. student, Roy Markham, gave the first report of TYMV as a virus "attacking" turnip, causing "bright yellow and green mosaic mottling" (Markham and Smith, 1946). Markham purified TYMV crystals, showed that they were a ribonucleoprotein complex, and that the virus accumulated to a high titer in plants—amounts at least equal to TMV in tobacco (Markham and Smith, 1946). Markham's early successes with TYMV can be attributed in part to being trained in biochemical research by Norman W. Pirie (Matthews, 1989), which directed him to nucleic acid and protein chemistry, and X-ray crystallography. Markham made significant advances in electron microscopy techniques (Matthews, 1981), one of which is among the most-cited plant virus papers in the first decade *Virology* (Markham et al., 1963).

Richard E. F. Matthews, following his demobilization from the New Zealand army at the end of World War II, pursued a Ph.D. at Cambridge from 1945 to 1948 (Elsden, 1982). Matthews "soon came under the influence" of Markham and "began spending a significant portion of [his] time working on TYMV" (Matthews, 1981). In working with Markham, a key player in ushering TYMV into the laboratory as an object for fundamental studies of RNA and protein chemistry, and Smith, a plant pathologist with expertise in general virology and insect transmission, Matthews obtained a superb education, which included access to the latest tools and techniques—radioisotopes, electrophoresis, super-centrifuges, crystallization, and electron microscopy—and all the expertise offered at Cambridge. By 1948, Matthews had co-authored a paper with Markham and Smith on a fundamental feature of TYMV: that by centrifugation a top (T)- and bottom (B)- component had been identified. By electrophoresis he confirmed that the B-component contained RNA; by crystal morphology and serology that the T- and B-components were indistinguishable; and, that TYMV was transmitted by the flea beetle (Markham et al., 1948). Matthews continued his research with TYMV for more than 35 years (Matthews, 1981).

Following his Ph.D. studies, Matthews returned to the University of Auckland, yet the close collaboration with Markham continued. Matthews (and TYMV) returned to Cambridge from 1952 to 1956, and later to the John Innes Institute (Norwich, England) after Markham became its director in 1967 (Matthews, 1989). Matthews is best remembered for his now classic textbook, "Plant Virology" (Matthews, 1970), which was the (only) plant virology textbook for several generations of plant virologists (Hull, 2014). "Plant Virology" was chock-full of physicochemical and plant physiology findings about Matthew's virus, TYMV, a physicochemical object seemingly far removed from its history as an economically important plant pathogen.

TYMV is an exemplar of an expanding number of viruses taken up for study in this 'middle period' of plant virology. The methods for purification of TMV and TYMV were followed by a focus on the chemistry of the virus, which was soon extended to *Tomato bushy stunt virus* (TBSV). As the tools and techniques matured, it was possible to do physicochemical studies of other viruses, including the many potato viruses (PVY, PVX, PYDV) and make further generalizations about viruses. Yet, in the early 1950s, virology was a young science. Luria reminded these workers that it was "… essential to keep constantly in mind in the study of virology that no conclusion based on the study of one virus can a priori be generalized as valid for any other virus. In view of the presumed heterogeneity of the objects that we call viruses, the greatest caution must be exerted in attributing to any one virus a property observed in another. This does not mean that we should consider each virus as a completely distinct entity, unrelated to any others" (Luria, 1953).

Table 1
Viruses studied in the first decade of *Virology*, 1955–1964[a].

Virus	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	Total
TMV[b]	8	12	12	14	13	21	19	30	28	25	182
PVY	2	0	2	1	3	2	3	7	2	1	23
PVX	2	0	2	1	1	2	6	3	3	1	21
CMV	0	1	1	2	1	3	2	2	5	3	20
WTV	1	0	1	0	0	0	4	4	2	3	15
TYMV	1	1	1	2	2	0	1	1	4	1	14
TNV	0	0	0	1	0	0	1	3	5	2	12
AlMV	0	0	0	0	0	1	3	0	1	3	8
TRSV	0	1	1	1	2	0	1	0	0	0	6
BSMV	0	0	0	1	3	0	0	0	1	1	6
PLRV	0	0	0	2	0	0	0	0	3	0	5
BCTV	1	1	1	1	0	0	0	0	0	1	5
SBMV	0	0	0	1	2	0	1	0	0	1	5

[a] The experimental use of a virus was determined by a survey of the abstract and results sections of papers published from 1955-1964. As this is a survey, the totals should be considered approximate. An arbitrary cutoff was 5 or more papers from 1955-1964. Viruses with four citations each were *Tomato bushy stunt virus* (TBSV), *Brome mosaic virus* (BMV), and *Tobacco etch virus* (TEV).

[b] Virus abbreviations in order are: *Tobacco mosaic virus* (TMV), *Potato virus Y* (PVY), *Potato virus X* (PVX), *Cucumber mosaic virus* (CMV), *Wound tumor virus* (WTV), *Turnip yellow mosaic virus* (TYMV), *Tobacco necrosis virus* (TNV), *Alfalfa mosaic virus* (AlMV), *Tobacco ringspot virus* (TRSV), *Barley stripe mosaic virus* (BSMV), *Beet curly top virus* (BCTV), and *Southern bean mosaic virus* (SBMV).

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