# PLANT VIROLOGY

edited by

M. K. CORBETT

and

H. D. SISLER

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*DR. L. O. KUNKEL—1884–1960*

## In Memoriam

# Editors' Preface

THIS BOOK has been compiled from a series of lectures and laboratory exercises presented during a Southern Regional Graduate Summer Session in Plant Virology, which was held at the University of Maryland, June 24 to August 2, 1963. The curriculum for the course was designed to provide students with the fundamentals and recent advances in the field of plant virology. The science of plant virology had its beginning near the end of the nineteenth century when Beijerinck described the filterable infectious extract from mosaic diseased tobacco plants as a virus or a *contagium vivum fluidum*. Today plant virology encompasses many disciplines as exemplified by the table of contents of this book. The subject matter ranges over a wide variety of topics including symptomatology, vector relationships, chemical nature, electron microscopy, and structure and substructure of viruses, which requires a student who wishes to master the science of virology to have a wide knowledge in the biological and physical sciences. It is difficult for one individual to accumulate sufficient knowledge to be an authority in all phases of virology. Thus, to cover each of these topics, specialists in the various areas were invited to participate in the course for periods of 1–2 weeks and present lectures and laboratory exercises in their field of specialization. Each lecturer prepared a review of his subject matter so that it would be available to a much larger audience than the 32 students enrolled from the 15 participating southern institutions. These lectures have been published in anticipation that they will stimulate further research and development in the science of virology. The need for a textbook of plant virology has long been evident by the number of review articles that have appeared in the last few years in many scientific journals. It is recognized that this text will not make a virologist out of a student but it is hoped that it will suffice as an introduction to the subject of plant virology and provide a stimulus for students to continue in the search for knowledge rather than to accept dogma.

The success of this course depended greatly upon the cooperation of the following to whom special recognition and acknowledgment is hereby given: to the Regional Committee of the Southern Regional Education Board for its work in the initial planning stages; to Drs. S. J. P. Chilton and J. P. Fulton, members of the Executive Committee, for assistance in preparing the curriculum, selection of lecturers, and preparation of the grant proposal; to Dr. William L. Bowden, Associate Director for Regional Programs, Southern Regional Education Board, who worked with the Regional and Executive Committees throughout the course of the project; to Dr. Ronald Bamford, Dean of

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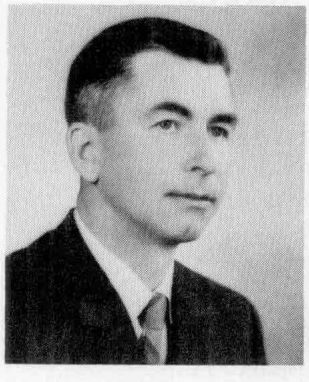

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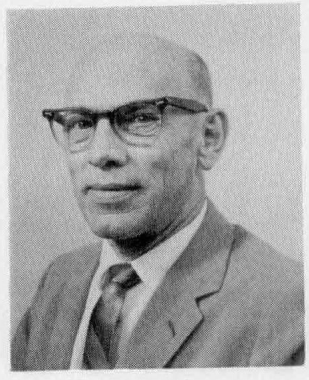

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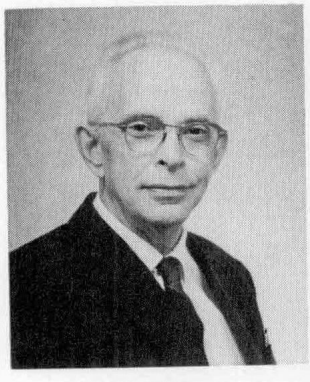

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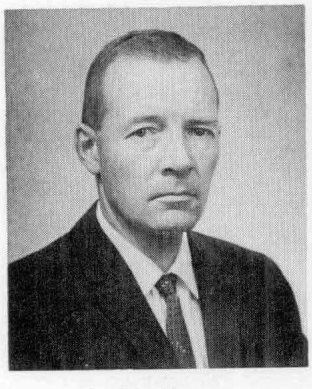

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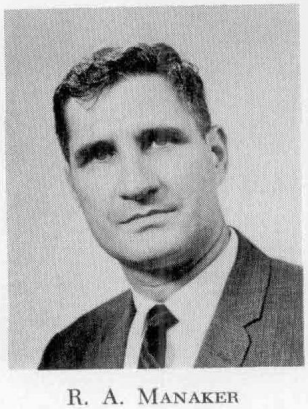

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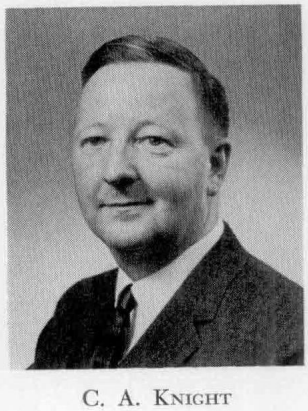

C. A. Knight

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M. K. CORBETT

# Introduction

THE WORD *virus* was described in the Phillips dictionary of 1720 as "a poison, venom, also a rammish smell as of the armpits; also a kind of watery matter, whitish, yellowish, and greenish at the same time, which issues out of ulcers and stinks very much; being indued with eating and malignant qualities." The modern concept of a virus as a pathogenic agent did not develop immediately, but required years of painstaking observation and research. By 1950, a virus was described by Bawden (1950) as an "obligately parasitic pathogen with dimensions of less than 200 mμ." Holmes (1948) proposed that viruses are "etiological agents of disease, typically of small size and capable of passing filters that retain bacteria, increasing only in the presence of living cells, giving rise to new strains by mutation, not arising *de novo*." Luria (1959) defined viruses as "submicroscopic entities, capable of being introduced into specific living cells and reproducing inside such cells only." Various other definitions have been proposed from time to time, but these few will suffice to demonstrate how the connotation of the word *virus* has been altered as knowledge has accumulated. In the following pages, I wish to show, by presenting some of the important findings, how this knowledge developed and how these discoveries have contributed to the present meaning of the word *virus* and to the science of virology.

Undoubtedly, many of the plant diseases which we now know are caused by viruses were recognized many years ago, but few of them attracted attention before the turn of the nineteenth century. Perhaps one of the oldest such plant diseases is that of tulip mosaic, or "breaking" as it was commonly called. The condition has been termed beneficial by some investigators because it induced color changes in the tulip flowers that enhance their beauty. They were so sought after by tulip fanciers during the sixteenth and seventeenth centuries that speculators gambling on the tulip market created the craze "tulipomania." Although the cause of the breaking was unknown at that time, planters knew how to transmit the condition by bulb grafts, and Blagrave in 1675 gave exact procedures and details for grafting such bulbs (McKay and Warner, 1933). The actual association of "breaking" with a virus had to wait until 1926 when it was shown that the virus could be transmitted mechanically and by aphids (McKay and Warner, 1933). Another early recognized plant virus disease was that of Jessamine (Jasminum) mottle. In a letter published in the philosophical transactions in 1720 Mr. Henry Cane reported that in 1692 he had transmitted the mottle condition to a common white Jasminum by grafting to it a yellow-striped Jasminum. In the words of Mr. Cane: "I have tried several other sorts of variegated

plants but do not find any of them transmute as that Jessamine will do." A similar situation was noted by Vibert in 1863 to occur in trees. He reported that apple trees budded with buds from "aucuba" plants produced variegated leaves on the stock the following spring. In some cases the buds failed, but the tree still produced variegated leaves. He concluded that the scion and stock need only be together long enough to allow sap to pass from the scion to the stock. He also reported a similar condition to occur in grafts between plants of rose and dog-rose.

## 1–1. DEVELOPMENT OF THE SCIENCE OF VIROLOGY

Virus diseases undoubtedly damaged many crop plants and ornamentals at this early date, but little was done to find their cause until the middle of the nineteenth century. Mayer (1886), an agricultural chemist working at Wageningen, the Netherlands, investigated a mosaic disease of tobacco, which had been termed "bunt," "rust," or "smut" by growers. To prevent confusion, Mayer suggested the international name of "mosaic disease of tobacco." The causal agent of the disease was unknown, though many theories had been proposed. Mayer attempted many experiments on the etiology of the mosaic disease and found that the causal agent was transmissible to healthy plants in juice extracts. He postulated that the disease was caused by an unorganized or organized ferment and that an unorganized ferment like an enzyme, capable of self-reproduction was unheard of. He found that continual heating at 60°C did not alter the infectivity but that it became weaker at 65°–75°C and was lost after several hours heating at 80°C. He was unable to retain infectivity after clarification and precipitation with weak alcohol. Thus, he concluded that the infectious agent was subject to the living conditions of organized ferments such as bacteria and fungi. Fungi were ruled out as the causal agent because they were too large to go through the filter paper. He concluded that the causal agent of the mosaic disease of tobacco was a bacterium about which little was known concerning its mode of life or infectious form. Peach yellows disease, according to Smith, may have been recognized as early as 1750, but nothing was known about the nature of the disease until 1891 when he showed that it was contagious, had a long incubation period, and was bud transmitted.

In 1890, Ivanowski (1892) noted two diseases of tobacco in the Crimea. One was a pox-disease, and the other a mosaic disease similar to that reported by Mayer. He believed that the two diseases were independent rather than different stages of one disease. He verified Mayer's results on transmission, thermostability, and the absence of fungi and other parasites. He did not agree with Mayer, however, with respect to his statement on filtration through double filter paper. Ivanowski's preparation was still infectious after filtering through double filter paper and he knew that such filtration would not retain bacteria. Furthermore, he found that his preparation was still infectious even after filtering through a Chamberland filter-candle that would retain bacteria. Ivanowski thought his results were due either to a toxin secreted by the bacteria or to the penetration of the bacteria through the pores of the filter. The cause of these unknown diseases was still thought to be corpuscular, but they were now known to be caused by agents transmissible mechanically and by grafting. The first departure from the corpuscular theory for the etiology of the tobacco mosaic disease came with the work of Beijerinck (1898), who concluded after experiments on agar diffusion that the disease was not caused by microbes but by a *contagium vivum fluidum*. He also concluded from serial inoculation that the contagium reproduced itself in the living plant. It is also in Beijerinck's work that the word *virus* is used to describe the contagium. He found that the virus would infect and invade young tissue more rapidly than mature tissue, moved in both the xylem and the phloem, was graft transmissible and able to infect plants by means of the roots. He also reported that the virus was still infectious after drying for two years in diseased leaves, would survive the winter in