

PLANT VIROLOGY

edited by

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and

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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

Preface

the Graduate School and former Head of the Department of Botany, University of Maryland, who served as representative of the Regional Advisory Council on Graduate Education in the Agricultural Sciences and made many valuable contributions at all stages of the program; to the University of Maryland, for so generously providing the necessary facilities for conducting the course; to the staff of the Botany Department, University of Maryland, for their assistance and cooperation; to the lecturers and students who made the course so suc-

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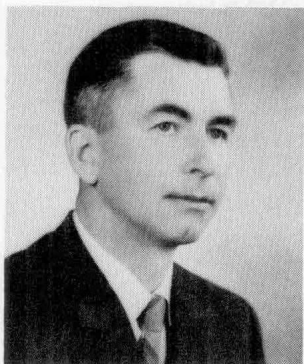
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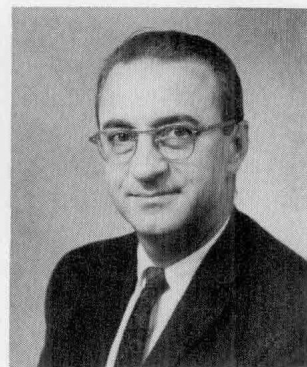
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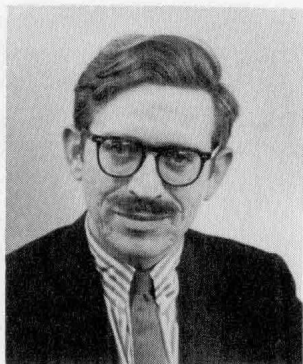
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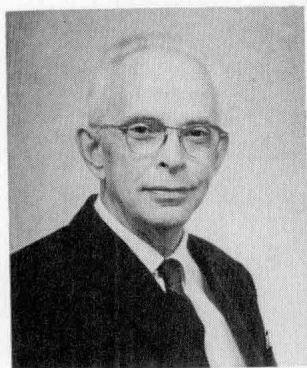
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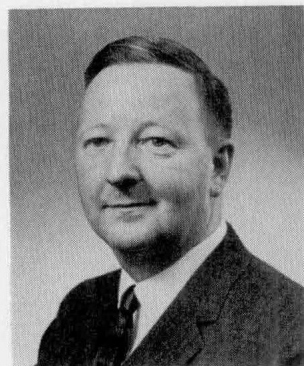
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Contents

xi

Contents

I. ABNORMALITIES OF LATEX FLOW	37
J. ABNORMALITIES OF GROWTH HABIT	37
2-9. MASKING OF SYMPTOMS	38
2-10. LITERATURE CITED	38

3—R. W. FULTON

Transmission of plant viruses by grafting, dodder, seed, and mechanical inoculation—39

3-1. INTRODUCTION	39
3-2. GRAFT TRANSMISSION	39
3-3. DODDER TRANSMISSION OF PLANT VIRUSES	42
A. THE MECHANISM OF DODDER TRANS- MISSION	42
B. PRACTICAL ASPECTS OF DODDER TRANSMISSION	43
C. METHODS OF USING DODDER	43
3-4. SEED TRANSMISSION OF PLANT VIRUSES	44
A. THE RATE OF VIRUS TRANSMISSION IN SEED	44
B. POLLEN TRANSMISSION	45
C. ELIMINATION OF VIRUS FROM SEED	45
D. LATENT VIRUS IN SEED	46
E. CORRELATION OF SEED TRANSMISSION WITH OTHER VIRUS CHARACTERISTICS	46
F. MECHANISMS RESTRICTING SEED TRANSMISSION	46
3-5. MECHANICAL INOCULATION	47
A. HISTORICAL	48
B. METHODS OF APPLYING INOCULUM	48
C. SPRAYING METHODS OF APPLYING INOCULUM	49
D. PRICKING AND INJECTION APPLICATION OF INOCULUM	49
E. HOST SUSCEPTIBILITY; THE USE OF ABRASIVES	50
F. PHYSIOLOGICAL FACTORS OF HOST SUSCEPTIBILITY	51
G. EFFECT OF ILLUMINATION	51
H. EFFECT OF HOST NUTRITION ON SUSCEPTIBILITY	52
I. EFFECT OF HEAT TREATMENTS ON SUSCEPTIBILITY	52
J. OTHER FACTORS AFFECTING SUSCEPTI- BILITY	53
K. INFECTIVITY OF INOCULUM; THE PHOSPHATE EFFECT	53
L. INHIBITORS IN PLANT EXTRACTS	54
M. POLYPHENOLS AND ANTIOXIDANTS	55
N. SOURCES OF INOCULUM	57
O. THE MECHANISM OF INFECTION AND FACTORS AFFECTING IT	57
P. RIBONUCLEASE AND VIRUS TRANS- MISSION	59
3-6. CONCLUSIONS	59
3-7. TABLES	60
3-8. LITERATURE CITED	63

4—A. F. ROSS

Identification of plant viruses—68

4-1. INTRODUCTION	68
4-2. ESTABLISHING THAT THE "UN- KNOWN" IS A VIRUS	69
4-3. ESTABLISHING THAT ONLY ONE VIRUS IS PRESENT	70
4-4. GENERAL APPROACH TO IDENTI- FICATION	71
4-5. TECHNIQUES AND TESTS USED IN IDENTIFICATION	72
A. SYMPTOMATOLOGY AND HOST RANGE	73
B. PROPERTIES IN CRUDE JUICE	77
C. TRANSMISSION CHARACTERISTICS	80
D. INTERACTION WITH OTHER VIRUSES	81
E. RESPONSE TO PRESENCE OF SPECIFIC GENES IN THE HOST	84
F. SEROLOGICAL TESTS	85
G. VIRUS PARTICLE CHARACTERISTICS	86
4-6. CHOICE OF CRITERIA TO USE IN ESTABLISHING THE IDENTITY OF AN "UNKNOWN"	88
4-7. VIRUS DESCRIPTIONS AND NAMES .	89
4-8. ROUTINE DIAGNOSES	90
4-9. LITERATURE CITED	91

5—W. C. PRICE

Strains, mutation, acquired immunity, and interference—93

5-1. INTRODUCTION	93
5-2. MUTATION	93
A. EVIDENCE FOR MUTATION	94
B. PERMANENCE OF MUTANTS	94
C. RATE OF MUTATION	95
D. CHARACTERISTICS ALTERED BY MUTATION	96
E. ARTIFICIAL INDUCTION OF MUTATION	97
5-3. HYBRIDIZATION	99
5-4. STRAINS	100
A. SIMILARITIES AND DIFFERENCES AMONG STRAINS	100
B. IDENTIFICATION OF STRAINS	101
C. NATURALLY OCCURRING STRAINS	102
D. USEFUL STRAINS	102
5-5. ACQUIRED IMMUNITY	103
A. ACQUIRED IMMUNITY FOLLOWING RECOVERY FROM DISEASE	104
B. CROSS PROTECTION	108
5-6. INTERFERENCE	110
A. INTERFERENCE RESULTING FROM USE OF MIXED INOCULA	111
B. INTERFERENCE WITHIN AN INOCU- LATED LEAF	111
C. LOCALIZED INTERFERENCE IN HYPERSENSITIVE HOSTS	112

Contents

D. SYSTEMIC INTERFERENCE IN HYPER-SENSITIVE HOSTS	112
E. INTERFERENCE BY INACTIVE VIRUS	114
5-7. LITERATURE CITED	114

6-B. D. HARRISON

The transmission of plant viruses in soil—118

6-1. INTRODUCTION	118
6-2. ECONOMIC IMPORTANCE OF SOIL-BORNE VIRUSES	119
6-3. GENERAL PROPERTIES OF THE VIRUSES	119
A. NEMATODE-TRANSMITTED VIRUSES WITH POLYHEDRAL PARTICLES (NEPO-VIRUSES)	121
B. NEMATODE-TRANSMITTED VIRUSES WITH TUBULAR PARTICLES (NETU-VIRUSES)	122
C. TOBACCO NECROSIS AND ALLIED VIRUSES	123
D. LETTUCE BIG-VEIN AND ALLIED VIRUSES	124
E. WHEAT MOSAIC AND ALLIED VIRUSES	125
F. TOBACCO MOSAIC VIRUS	126
6-4. METHODS OF TRANSMISSION	126
A. TRANSMISSION BY NEMATODES	126
B. FUNGUS-ASSISTED TRANSMISSION	132
C. METHOD OF TRANSMISSION UNKNOWN	135
6-5. VIRUS ECOLOGY	137
A. METHODS OF SURVIVAL	137
B. DISTRIBUTION AND SPREAD	138
C. INCIDENCE OF INFECTION	140
6-6. METHODS OF CONTROL	141
A. PREVENTION OF SPREAD TO NEW SITES	141
B. CONTROL MEASURES ON INFESTED LAND	142
6-7. CONCLUDING REMARKS	144
6-8. LITERATURE CITED	144

7-R. H. E. BRADLEY

Aphid transmission of stylet-borne viruses—148

7-1. INTRODUCTION	148
7-2. FRAMEWORK	149
A. APHIDS	151
B. VIRUSES	153
C. PLANTS	154
7-3. UPTAKE	155
A. DURING SUPERFICIAL PROBES	155
B. WHERE ON THE SOURCE?	156
C. HOW IS THE LABIUM PLACED IN RELATION TO THE EPIDERMAL CELLS?	157

D. IS UPTAKE FROM WITHIN OR BETWEEN EPIDERMAL CELLS?	157
E. SALIVA?	158
F. UPTAKE OTHER THAN DURING SUPERFICIAL PROBING?	159
G. WHY DOES UPTAKE MAINLY OCCUR DURING SUPERFICIAL PROBING?	160
H. EFFECT OF KEEPING APHIDS OFF PLANTS PRIOR TO UPTAKE	162
I. SUNDRIES	163
7-4. CARRY OVER	164
A. ON PLANTS	164
B. OFF PLANTS	166
C. STYLET TREATMENTS	167
7-5. INOCULATION	170
7-6. LITERATURE CITED	173

8-KARL MARAMOROSCH

Virus-vector relationships: Vectors of circulative and propagative viruses—175

8-1. APHIDS	175
8-2. TREEHOPPERS	177
8-3. MITES	178
8-4. WHITEFLIES	178
8-5. MEALYBUGS	179
8-6. THRIPS	179
8-7. LEAFHOPPERS	180
A. CIRCULATIVE TRANSMISSION	180
B. PROPAGATIVE TRANSMISSION	180
C. VIRUS INTERRELATIONSHIPS AND VIRUS STRAINS	182
D. LOSS OF TRANSMISSIBILITY	184
E. VIRUS ACQUISITION AND TRANSMISSION	184
F. VIRUS INTERRELATIONSHIPS	185
G. SEROLOGY	185
8-8. EFFECTS OF PLANT VIRUSES ON VECTORS AND NONVECTORS	186
A. ASTER YELLOWS VIRUS	186
B. RICE VIRUSES	187
8-9. PLANT VIRUSES PATHOGENIC TO THEIR VECTORS	187
A. EUROPEAN WHEAT STRIATE MOSAIC VIRUS	188
B. RICE DWARF VIRUS	188
8-10. BENEFICIAL VIRUS EFFECTS	189
8-11. CONCLUSIONS	190
8-12. LITERATURE CITED	191

9-D. A. ROBERTS

Local-lesion assay of plant viruses—194

9-1. INTRODUCTION	194
9-2. METHODS FOR ASSAYING PLANT VIRUSES	194
A. PHYSICAL	195

Contents

<p>B. CHEMICAL 196</p> <p>C. SEROLOGICAL 196</p> <p>D. BIOLOGICAL 197</p> <p>9-3. THE LOCAL-LESION ASSAY 198</p> <p style="padding-left: 20px;">A. THE DILUTION CURVE 198</p> <p style="padding-left: 20px;">B. ASSESSING RELATIVE INFECTIVITY 200</p> <p style="padding-left: 20px;">C. FACTORS INFLUENCING THE LOCAL-LESION ASSAY 205</p> <p>9-4. DISCUSSION 208</p> <p>9-5. LITERATURE CITED 209</p> <p style="text-align: center;">10-R. L. STEERE</p> <p style="text-align: center;">Purification—211</p> <p>10-1. INTRODUCTION 211</p> <p>10-2. HOST SELECTION 211</p> <p style="padding-left: 20px;">A. ASSAY HOST 211</p> <p style="padding-left: 20px;">B. PRODUCTION HOST 211</p> <p>10-3. DETERMINATION OF INITIAL BUFFER 212</p> <p>10-4. MACERATION OF INFECTED TISSUES AND JUICE EXTRACTION 212</p> <p>10-5. REMOVAL OF CONTAMINANTS 213</p> <p style="padding-left: 20px;">A. CLARIFICATION OF THE EXTRACT 214</p> <p style="padding-left: 20px;">B. FURTHER PURIFICATION OF CLARIFIED EXTRACTS 217</p> <p>10-6. CONCENTRATION PROCEDURES 228</p> <p style="padding-left: 20px;">A. REMOVAL OF SOLVENT FROM THE SUSPENSION 228</p> <p style="padding-left: 20px;">B. REMOVAL OF VIRUS FROM SUSPENSION 230</p> <p>10-7. STORAGE OF PURIFIED VIRUS 231</p> <p>10-8. DETECTION OF IMPURITIES 231</p> <p style="padding-left: 20px;">A. ELECTROPHORESIS 232</p> <p style="padding-left: 20px;">B. ELECTRON MICROSCOPY 232</p> <p style="padding-left: 20px;">C. ULTRACENTRIFUGATION 232</p> <p style="padding-left: 20px;">D. DENSITY-GRADIENT CENTRIFUGATION 232</p> <p style="padding-left: 20px;">E. CHROMATOGRAPHY 232</p> <p style="padding-left: 20px;">F. AGAR-GEL FILTRATION 232</p> <p>10-9. SAMPLE PROCEDURE FOR PURIFYING VIRUS PARTICLES AND KEEPING THEM IN SUSPENSION THROUGHOUT PURIFICATION AND CONCENTRATION 232</p> <p>10-10. LITERATURE CITED 234</p> <p style="text-align: center;">11-ELLEN M. BALL</p> <p style="text-align: center;">Serology: Techniques used in plant virus research—235</p> <p>11-1. INTRODUCTION 235</p> <p>11-2. IMMUNIZATION TECHNIQUES 237</p> <p style="padding-left: 20px;">A. INTRAVENOUS INJECTION 237</p> <p style="padding-left: 20px;">B. INTRAMUSCULAR INJECTION IN FREUND'S ADJUVANT 238</p> <p style="padding-left: 20px;">C. COMPARATIVE STUDIES AND COMBINATIONS OF ROUTES OF INJECTION 238</p>	<p>D. ADJUVANTS OTHER THAN FREUND'S OIL EMULSION 239</p> <p>E. ACQUISITION OF BLOOD SAMPLES 239</p> <p>11-3. SEROLOGICAL TECHNIQUES 241</p> <p style="padding-left: 20px;">A. DILUTION END-POINT PROCEDURES 241</p> <p style="padding-left: 20px;">B. AGAR DIFFUSION PROCEDURES 245</p> <p style="padding-left: 20px;">C. CONJUGATED ANTIBODY PROCEDURES 247</p> <p>11-4. APPLICATION 248</p> <p>11-5. LITERATURE CITED 250</p> <p>11-6. SUPPLEMENTARY READING 252</p> <p style="text-align: center;">12-C. E. HALL</p> <p style="text-align: center;">Electron microscopy: Principles and application to virus research—253</p> <p>12-1. INTRODUCTION 253</p> <p>12-2. THE ELECTRON MICROSCOPE 254</p> <p>12-3. IMAGE CHARACTERISTICS 256</p> <p style="padding-left: 20px;">A. FOCUS 256</p> <p style="padding-left: 20px;">B. SCATTERING 258</p> <p style="padding-left: 20px;">C. GENERAL CONSIDERATIONS 258</p> <p>12-4. TECHNIQUES 259</p> <p style="padding-left: 20px;">A. SHADOW CASTING 259</p> <p style="padding-left: 20px;">B. STAINING 261</p> <p style="padding-left: 20px;">C. OTHER TECHNIQUES 262</p> <p>12-5. MICROSCOPY OF PLANT VIRUSES 263</p> <p style="padding-left: 20px;">A. TOBACCO MOSAIC VIRUS 263</p> <p style="padding-left: 20px;">B. SPHERICAL VIRUSES 263</p> <p>12-6. LITERATURE CITED 266</p> <p style="text-align: center;">13-D. L. D. CASPAR</p> <p style="text-align: center;">Structure and function of regular virus particles—267</p> <p>13-1. INTRODUCTION 267</p> <p>13-2. DESIGN PRINCIPLES AND SELF-ASSEMBLY 268</p> <p>13-3. STRUCTURAL CLASSIFICATION AND INTERRELATIONS OF VIRUSES 270</p> <p>13-4. VIRUS SUBSTRUCTURE AND THE X-RAY DIFFRACTION METHOD 271</p> <p>13-5. SYMMETRY AND MOLECULAR MORPHOLOGY OF TOBACCO MOSAIC VIRUS 275</p> <p style="padding-left: 20px;">A. HELICAL ARRANGEMENT OF SUB-UNITS 275</p> <p style="padding-left: 20px;">B. INTERNAL STRUCTURE 277</p> <p style="padding-left: 20px;">C. DEFORMED HELICAL STRUCTURES 279</p> <p style="padding-left: 20px;">D. SYMMETRY AND STRUCTURE OF POLYMERIZED PROTEIN 280</p> <p>13-6. ASSEMBLY OF THE TOBACCO MOSAIC VIRUS PARTICLE 282</p> <p>13-7. DESIGN OF ICOSAEDRAL VIRUS PARTICLES 285</p> <p>13-8. LITERATURE CITED 290</p>
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Contents

14—C. A. KNIGHT

Structural biochemistry of plant viruses—292

14-1. INTRODUCTION	292
14-2. COMPOSITION OF VIRUSES	292
A. GENERAL FEATURES AND RELATIONS AMONG THE MAJOR CLASSES OF VIRUSES	292
B. PLANT VIRUSES	293
14-3. STRUCTURE OF VIRUSES	295
A. SUBDIVISIONS OF PROTEIN STRUCTURE	295
B. PREPARATION OF VIRAL PROTEINS	296
C. SOME PROPERTIES OF VIRAL PROTEINS	296
D. PRIMARY STRUCTURAL CHARACTER- ISTICS OF SOME VIRAL PROTEINS	297
E. SECONDARY, TERTIARY, AND QUAT- ERNARY STRUCTURES	300
F. METHODS FOR PREPARING PLANT VIRUS NUCLEIC ACIDS	302
G. SUBDIVISIONS OF NUCLEIC ACID STRUCTURE	302
H. RECONSTITUTION OF VIRUS FROM ITS COMPONENTS	306
14-4. VIRUS MUTANTS	306
A. SPONTANEOUS MUTANTS	307
B. CHEMICALLY INDUCED MUTANTS	309
C. THE CODING RELATIONSHIP	311
14-5. LITERATURE CITED	313

15—W. N. TAKAHASHI

The biochemistry of virus infection—315

15-1. INTRODUCTION	315
15-2. CONCEPTS OF NATURE OF PLANT VIRUS MULTIPLICATION	315
A. OLD CONCEPT	315
B. NEW CONCEPT	315
C. BIPARTITE SYNTHESIS OF VIRUS	316
15-3. INFECTION PROCESS	316
A. ADSORPTION PHASE	316
B. THE INFECTIOUS ENTITY	316
C. SHEDDING OF PROTEIN COAT	317
D. HYPERACTIVITY OF THE NUCLEUS	317
15-4. VIRUS PROTEIN	318
A. MACROMOLECULAR NONINFECTIOUS PARTICLES	318
B. TOP COMPONENT OF TURNIP YELLOW MOZAIC VIRUS PREPARATION	318
C. ANOMALOUS PROTEIN OF TMV INFECTION	319
D. SOME PROPERTIES OF THE VIRUS PROTEIN	319
E. THE ROLE OF THIS PROTEIN IN THE BIOSYNTHESIS OF VIRUS	319
15-5. PROTEIN SYNTHESIS	321
A. STRUCTURE OF PROTEIN	321
B. SYNTHESIS IN NORMAL CELLS	321

C. RIBOSOMES	321
D. MECHANISM OF PROTEIN SYNTHESIS	321
E. REACTION MIXTURE	322
F. PROTEIN SYNTHESIS WITH ISOLATED PEA RIBOSOMES	322
G. PROTEIN SYNTHESIS WITH ISOLATED RIBOSOMES OF <i>E. coli</i>	322
H. SYNTHESIS OF TMV PROTEIN USING TMV-RNA AS MESSENGER	323
I. FAILURE TO FORM TMV PROTEIN WITH RIBOSOMES OF PLANT ORIGIN	323

15-6. INFECTIOUS VIRUS NUCLEIC ACID 323

A. INTEGRITY OF INFECTIOUS RNA	323
B. TMV-RNA	324
C. REPLICATION OF RNA	324
D. RNA POLYMERASES	325
E. EXPERIMENTS REPORTING SYNTHESIS OF INFECTIOUS RNA	325

15-7. DISCUSSION 327

15-8. LITERATURE CITED 328

16—L. BROADBENT

Control of plant virus diseases—330

16-1. EPIDEMIOLOGY 330

A. IDENTITY OF VIRUS	330
B. SOURCE OF VIRUS	330
C. HOST SUSCEPTIBILITY	333
D. IDENTITY AND EFFICIENCY OF VEC- TORS	334
E. ACTIVITY OF VECTORS	335

16-2. EXCLUSION AND PROTECTION—

I. INTRODUCTION OF VIRUSES INTO CROPS BY MAN, MAMMALS, AND BIRDS 337

A. VIRUSES SPREAD BY CONTACT	337
B. PROTECTED CROPPING	337
C. HYGIENE MEASURES	337
D. VIRUS INHIBITORS AND INACTIVATORS	338
E. CULTURAL MODIFICATIONS	339
F. INFECTION WITH MILD VIRUS STRAINS	339
G. VIRUSES INTRODUCED IN VEGETA- TIVELY PROPAGATED PLANT PARTS	339
H. SEED INFECTION	341

16-3. EXCLUSION AND PROTECTION—

II. INTRODUCTION OF VIRUSES IN- TO CROPS BY INSECTS AND MITES 342

A. PROTECTED CROPPING	342
B. BARRIER AND COVER CROPS	342
C. ISOLATION	343
D. FIELD SIZE	345
E. PLANT SPACING	345
F. ELIMINATION OF EXTERNAL SOURCES OF VIRUS OR VECTOR	346
G. BREAKING IN CROP CYCLES	347
H. AVOIDANCE OF VECTORS	348
I. INFECTION WITH MILD STRAINS OF VIRUS	349

Contents

J. KILLING VECTORS BEFORE THEY ENTER THE CROP	349	C. INFORMATION TRANSFER: REPLICATION, TRANSCRIPTION, TRANSLATION	390
K. KILLING VECTORS AFTER ARRIVAL	350	D. MOLECULAR BASIS OF GENETIC HOMOMOLOGY	392
16-4. ERADICATION OF VIRUS	351	E. THE NIRENBERG-OCHOA CODES	393
A. ERADICATION FROM SOIL	351	18-3. GENERAL TAXONOMIC CONSIDERATIONS	395
B. ERADICATION FROM SEEDS	351	A. WHAT IS TAXONOMY?	396
C. ERADICATION FROM VEGETATIVELY PROPAGATED MATERIAL BY HEAT	352	B. WHAT IS A CHARACTER?	396
D. ERADICATION BY TIP CULTURE	353	C. POWER OF THE MOLECULAR APPROACH THROUGH NUCLEIC ACIDS	398
E. ERADICATION BY ROGUING	353	D. HOMOMOLOGY CRITERIA BASED ON NUCLEIC ACIDS	399
F. ERADICATION BY CHEMICAL TREATMENTS	355	E. OTHER MOLECULAR APPROACHES: GENETICS AND PROTEINS	402
16-5. ERADICATION OF VECTORS	355	18-4. BACTERIA AND THE MUTUAL VALIDATION OF CLASSICAL AND MOLECULAR TAXONOMY	405
A. ERADICATION OF VECTORS WITHIN CROPS BY INSECTICIDES	355	18-5. VIRAL TAXONOMY	408
B. ERADICATION BY PREDATORS AND PARASITES	357	A. A BRIEF ORIENTATION	408
C. ERADICATION OF VECTORS IN SOIL BY CHEMICALS	357	B. SOME RECENT MOLECULAR-TAXONOMIC STUDIES	410
16-6. PLANT IMMUNITY AND TOLERANCE	357	C. A NEOCLASSICAL SYSTEM OF VIRUSES	415
A. USE OF IMMUNE OR TOLERANT VARIETIES OF PLANTS	357	18-6. PROSPECTS AND SPECULATIONS	417
B. PLANT AGE AT THE TIME OF INFECTION	358	A. TAXONOMIC DISCREPANCIES AND VIRAL EVOLUTION	417
C. CONTROL BY ALTERING NUTRITION	359	B. DIRECTION OF MOLECULAR EVOLUTION	420
16-7. CONCLUSION	359	18-7. SUMMARY	421
16-8. LITERATURE CITED	360	18-8. LITERATURE CITED	423
17-F. C. BAWDEN			
Speculations on the origins and nature of viruses-365			
17-1. INTRODUCTION	365	A1-M. A. LAUFFER	
17-2. CHANGING IDEAS ABOUT VIRUSES	366	Form and function: A problem in virology-427	
17-3. THE ORIGINS OF VIRUSES	368	A1-1. INTRODUCTION	427
A. THE IRRELEVANCE OF POTATO PARACRINKLE	368	A1-2. THE OPERATIONAL APPROACH	428
B. CHANGES IN THE BEHAVIOUR OF NUCLEIC ACIDS	369	A1-3. METHODS FOR IDENTIFYING FORM WITH FUNCTION	429
17-4. INFECTION AND MULTIPLICATION	374	A. CORRELATION OF INFECTIOUSNESS WITH CHARACTERISTIC PARTICLE	429
A. ESTABLISHING INFECTION	377	B. FRACTIONATION	430
B. SYNTHESIS AND ASSEMBLY	379	C. DIFFUSION COEFFICIENT	430
17-5. GENETIC VARIABILITY	381	D. DESTRUCTION OF INFECTIOUSNESS	430
17-6. LITERATURE CITED	384	E. ULTRAFILTRATION	430
18-FRANK LANNI			
Viruses and molecular taxonomy-386			
18-1. INTRODUCTION	386	F. ULTRACENTRIFUGATION	431
18-2. CONCEPTUAL BACKGROUND OF MOLECULAR TAXONOMY	387	G. ELECTROPHORETIC MOBILITY	431
A. ORGANIZATION OF GENETIC INFORMATION: CODING RELATIONS	387	H. CHROMATOGRAPHY	432
B. HEREDITARY VARIATION: EFFECTS OF MUTATION	389	A1-4. SOUTHERN BEAN MOSAIC VIRUS	432
A2-K. M. SMITH			
Virus diseases of arthropods-439			
A2-1. INTRODUCTION	439	A1-5. TOBACCO MOSAIC VIRUS RNA	435
A2-2. TYPES OF ARTHROPOD VIRUSES	439	A1-6. LITERATURE CITED	438

Contents

<p>A. NUCLEAR POLYHEDROSES 440</p> <p>B. CHEMICAL COMPOSITION OF THE NUCLEAR POLYHEDROSIS VIRUSES AND THEIR POLYHEDRA 440</p> <p>C. CYTOPLASMIC POLYHEDROSES 441</p> <p>D. THE GRANULOSSES 443</p> <p>E. CHEMICAL COMPOSITION 443</p> <p>F. THE FREE VIRUSES 444</p> <p>A2-3. ORDERS IN WHICH VIRUSES HAVE BEEN DESCRIBED 444</p> <p>A2-4. DESCRIPTION OF SOME VIRUS DISEASES OF ARTHROPODS 445</p> <p style="padding-left: 20px;">A. CHEMICAL COMPOSITION 446</p> <p>A2-5. ISOLATION AND PURIFICATION 447</p> <p>A2-6. MORPHOLOGY AND ULTRASTRUCTURE 449</p> <p>A2-7. METHODS OF SPREAD 449</p> <p>A2-8. LATENT VIRUS INFECTIONS 450</p> <p>A2-9. TRANSMISSION BETWEEN DIFFERENT SPECIES AND ORDERS 452</p> <p>A2-10. VIRUSES MULTIPLYING IN PLANTS AND INSECTS 453</p> <p>A2-11. LITERATURE CITED 455</p> <p style="text-align: center; padding: 10px 0;">A3—R. A. MANAKER</p> <p>An introduction to the tumor viruses—457</p> <p>A3-1. INTRODUCTION 457</p> <p>A3-2. THE AVIAN-TUMOR VIRUSES 457</p> <p style="padding-left: 20px;">A. FOWL LEUCOSIS 457</p> <p style="padding-left: 20px;">B. AVIAN SARCOMA VIRUSES 459</p> <p>A3-3. THE MURINE GROUP OF TUMOR VIRUSES 469</p> <p style="padding-left: 20px;">A. INTRODUCTION 469</p>	<p>B. THE MOUSE MAMMARY TUMOR AGENT 470</p> <p>C. MURINE LEUKEMIA VIRUSES 474</p> <p>D. THE CROSS VIRUS 475</p> <p>E. THE GRAFFI VIRUS 476</p> <p>F. THE FRIEND VIRUS 477</p> <p>G. THE MOLONEY VIRUS 478</p> <p>H. THE SCHOOLMAN-SCHWARTZ AGENT 479</p> <p style="padding-left: 20px;">I. THE RAUSCHER VIRUS 479</p> <p style="padding-left: 20px;">J. THE C-60 VIRUS 479</p> <p style="padding-left: 20px;">K. OTHER LEUKEMOGENIC AGENTS 479</p> <p style="padding-left: 20px;">L. LEUKEMOGENIC AGENTS IN TISSUE CULTURE 480</p> <p style="padding-left: 20px;">M. LEUKEMIA VIRUS MORPHOLOGY 480</p> <p style="padding-left: 20px;">N. POLYOMA VIRUS TUMORS IN MICE 481</p> <p>A3-4. OTHER VIRUSES THAT INDUCE TUMORS IN RODENTS 485</p> <p style="padding-left: 20px;">A. SIMIAN VIRUS 40 485</p> <p style="padding-left: 20px;">B. ADENOVIRUS 487</p> <p>A3-5. RABBIT TUMOR VIRUSES 487</p> <p style="padding-left: 20px;">A. SHOPE RABBIT PAPILLOMA VIRUS 487</p> <p style="padding-left: 20px;">B. THE RABBIT FIBROMA VIRUS 489</p> <p>A3-6. YABA VIRUS 491</p> <p>A3-7. PLANT TUMOR VIRUSES 491</p> <p style="padding-left: 20px;">A. THE WOUND-TUMOR VIRUS 491</p> <p>A3-8. OTHER TUMOR VIRUSES 492</p> <p>A3-9. VIRUSES ASSOCIATED WITH HUMAN LEUKEMIA 492</p> <p>A3-10. LITERATURE CITED 494</p> <p style="text-align: center; padding: 10px 0;">Bibliographical index—501</p> <p style="text-align: center; padding: 10px 0;">Subject index—515</p>
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THE WORD *virus* was described in the Phillips dictionary of 1720 as "a poison, venom, also a rammish smell as of the arm-pits; also a kind of watery matter, whitish, yellowish, and greenish at the same time, which issues out of ulcers and stinks verv 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 m μ ." 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.

1

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