Watson, M. A. 1969. *Viruses, vectors and vegetation [Book Review].* Fisons Pest Control Limited.

book reviews

Viruses, Vectors and Vegetation

edited by **Karl Maramorosch,**

Interscience Publishers (John Wiley & Sons), New York, London, Sydney, Toronto
657 pp.; 80 text figures; 30 tables; 1969; 281*s*

Reviewed by **Dr M A Watson**
Rothamsted Experimental Station, Harpenden, Herts

Viruses, Vectors and Vegetation is not a very suitable title for this book, partly because it suggests a semi-popular scientific work such as the trend-setting *Rats, Lice and History* (Zinsser, 1943) or *Fleas, Flukes and Cuckoos* (Rothschild and Clay, 1952), whereas it is a collection of papers by specialists and would not be easily understood without some background of information. Also the 'Viruses' of the title is not strictly accurate because some of the diseases discussed are now believed to be caused not by viruses but by organisms resembling Mycoplasmata. This is mentioned (with references) by Shikata and Maramorosch but not till page 409. The reasons might better have been given in the Preface (dated 1969) so that they could have been borne in mind by the reader throughout the book. Nothing in the contributions is invalidated except some of the titles, because everything known about this category of pathogens is behavioural, but many of our beliefs about leaf-hopper transmitted viruses are based on information obtained with pathogens that may not be viruses, and some re-adjustment will have to be made. Nevertheless the book remains an excellent collection of papers on subjects concerned with the transmission of plant viruses, needing no gimmickry to recommend it.

The Editor (Dr Karl Maramorosch), refers to it obliquely, in his preface as a Textbook, but only half the papers are really intended as works of reference, many are platforms for the author's own ideas and sometimes prejudices. They are none the worse for that so long as the background is understood, because many aspects of the subjects are well served and there is often more lively and interesting presentation than in conventional Textbooks. These, indeed, often [illegible] h yellow reading, for the effort of cc[illegible] virus much of the enthusiasm o[illegible] ults index is a great leveller. [illegible] d-

The preface also expl[illegible] of a Conference held in Tok[illegible] and United States scientists; 24 of [illegible] in the volume are by North American or Japa[illegible] In 1965 the vectors discussed were almost all leaf hopp[illegible] but the scope was extended in 1966 when it was decided to publish the papers. To quote the Preface 'In addition to the topics discussed in Tokyo, which were brought up to date and broadened considerably, additional chapters now cover virus-purification and bioassay . . . specificity of aphid-borne viruses, aphid-vector morphology; nematode, fungus and mite-transmission' . . . (also white flies which the editor forgot to mention) . . . 'nonpersistent leaf-hopper borne viruses, fluorescent antibody studies, virus diseases of maize and disease control'.

Although the chapters are the works of well-known experts, and are often labours of love, the collection is sometimes confusing because one cannot easily disentangle particular themes and controversies. Each paper is usually a well-informed and stimulating essay on a particular topic, but, in common with most publications derived from symposia, it may be difficult to evaluate, or even to relate, different interpretations of the same facts. For example, the vector specificity discussed by Oman in the opening chapter, on what might be called a global level, seems to bear little relation to the behaviour of strains and isolates of barley yellow dwarf viruses in different aphid species, so intelligibly presented by Rochow. Rochow's story has unexpected links with the section of Freitag's paper dealing with Dependent Transmission, and both with the closing paragraphs of Everett and Lamey's paper on hoja blanca of rice.

Again, the structures described by Forbes and MacCarthy need the contributions of Pirone, Sylvester, Nishi and others to explain their significance. Not everyone will be able to read through from the beginning and memorise all the clues. Even those who do may have to think matters out for themselves but they should derive benefit and entertainment from the exercise.

The chapters are not numbered; it might be useful if they were, but what would be chapters two to five are typical review articles, well written and well illustrated, evaluating past work, bringing it up to date with recent and unpublished results, and discussing the future. Three of the papers, those by Teakle on fungus vectors, Cadman and Taylor on nematodes and Slykhuis on mites, have their tasks made easier by the subjects being so recent that almost the whole of the literature is still in use and can be discussed familiarly. The authors were involved with the original discoveries, and have been close to the research from the beginning.

The white fly transmitted viruses reviewed by Costa have a much longer history, but much of the earlier work was epidemiological and Costa has concentrated on the manner of transmission, making a surprisingly coherent story from rather scattered information. Work by M. A. and J. J. Nour in the Sudan has not been noticed. Two articles are about purely entomological aspects of the relation between insects and plant viruses. Forbes and MacCarthy summarise their own and other work on the morphology and feeding of aphids and (in less detail) leafhoppers, with new illustrations of the head and mouth parts of aphids around which so much controversy about virus transmission is centred but nothing new has emerged. T. Ishara does for the Auchenorrhyncha some of what Kennedy, Day and Eastopp's 'Conspectus' (*q.v.*) did for the Aphidoidea. Ishara gives a classified list of 131 species of leaf- and plant-hoppers and the diseases they transmit; a most useful contribution that has already helped the writer of this review.

Professor Fukushi's authoritative review of his own and his students' work on rice viruses is especially welcome, both for its content, and also, because the subject owes so much to his early researches, for its historical importance. R. Granados, writing on the diseases of maize, has been at pains to emphasize new aspects of the relations between the diseases and their vectors, and gives us the only illustration (not a very clear one) of 'bacilliform' particles (of maize mosaic virus). This shape of particle is now known to be associated with many persistent aphid and leafhopper-transmitted viruses including lettuce necrotic yellows, sowthistle yellow vein (Sylvester *q.v.*) and Russian winter wheat mosaic viruses (Razvjazkina *et al.*, 1968, 1st Congress of Plant Pathology), as well as human, animal and insect-pathogenic viruses. Perhaps their association with plant viruses is too recent for them to be discussed in this volume. Corn stunt 'virus', discussed here and in other papers, is one of those now believed to be mycoplasmal.

Jensen's paper on *Insect-Diseases Induced by Plant-Pathogenic viruses* includes some presumed mycoplasmal diseases, e.g. Aster yellows and Rice yellow dwarf. Even the carefully documented Western X disease (peach yellow leaf roll) is of uncertain status, as no recognizable virus particle has so far been described for it. However results for rice stunt virus, winter wheat mosaic and some aphid-transmitted viruses, confirm that the effects can be caused by both kinds of plant-pathogen. Much of Freitag's paper on – *Interactions of Plant Viruses and Virus Strains In Their Insect Vectors* is also concerned with corn stunt and aster yellows diseases.

Everett and Lamey describe the properties and attributes of hoja blanca disease of rice in the only article devoted to a single pathogen. The symptoms and host range, and the transmission which can be transovarial, by the delphacid vector *Sogatodes oryzicola* strongly resemble those of European wheat striate mosaic (Slykhuis and Watson, 1958). This and other such pathogens could have a common ancestor, and the author's hypothesis that different species of vectors became adapted to spreading hoja blanca strains among different weeds and cultivated hosts may have a wider connotation than they claim. Similar adaptations probably account for much of the vector specificity described by other contributors.

Two papers are concerned with epidemiology and control. Broadbent in *Disease Control through Vector Control* summarizes most of the relevant work on the control of aphids and other vectors, particularly by pesticides. Some new methods, for example oil sprays to prevent the probing of aphids, are discussed, but not host-plant resistance against vectors although some progress is being made towards its use. Reference to virus-resistance in plants is excluded by the Title, unfortunately, because plant breeding has contributed greatly towards control, particularly of hopper-borne viruses which are often not easily controlled by insecticides. The use of prediction of virus outbreaks from weather and phenotypic phenomena is briefly discussed but more might have been said of this important trend.

Floyd Smith and Webb describe a novel aphid-deterrent which Smith was largely concerned in developing. It consists of a white or silvery reflecting surface surrounding beds, or between rows, of crops, which discourages aphids from landing. It has been tested successfully in Europe and elsewhere and is a useful development of studies by Moericke (1954; *q.v.*) and others during the last decade, on the responses of aphididae to light and colour.

Brakke's excellent contribution, *Isolation and Purification of Vector-Borne Plant Viruses* is both a work of reference and a treatise on methods, with a Bibliography nearly half as long as the paper. It is difficult to imagine how more information could have been compressed into the space. A similar compendium of useful information is N. Suzuki's *Purification of Single and Double-stranded Vector-borne* RNA *Viruses* largely concerned with hopper-transmitted wound tumour and rice dwarf viruses and aphid-transmitted pea enation mosaic. The first two have double-stranded RNA and the third, single stranded; perhaps this accounts for the diversity of their behaviour. Suzuki believes that once a virus has been purified it is easy to test whether it is propagative or not. A corollary is that until an infective agent has been isolated and purified it is difficult to tell even whether it is a virus or not.

Four useful papers deal with special techniques needed, or useful, for the investigation of viruses. Sinha describes isolation of infective organs, and the use of fluorescent antibody in detecting the localities of disease agents within the bodies of vectors.

A chapter by Mitsuhashi on methods for growing plant viruses in insect tissue culture should be of great interest because the technique is new in this field and not many workers can manage it yet. According to Saito, haemagglutination tests using barley stripe mosaic virus as the antigen, are about 10,000 times more sensitive than ordinary serum precipitation techniques. He believes that such tests will be useful to detect early outbreaks of virus-disease in crops, as well as in more academic research.

Whitcombe describes injection and artificial feeding techniques used to measure the fluctuations in virus concentration in vector-leafhoppers, and of viruses *in vitro* in plant or insect extracts. His main example is the western X-disease agent. Agent seems to be the fashionable term for a disease of uncertain etiology.

Several papers deal with electron microscopy of ultra-thin sections. The use of this technique, developed only during the past decade, has greatly increased our understanding of vector-transmitted plant viruses, and it promotes the discovery that some are mycoplasms. I place first the contribution that pleased me most, Sochow Nasu's description of the entry of rice dwarf virus particles into the eggs of the vector, *Nephotettix cinciteps*, through the micropyle with the invading mycetocytes. It was always a favourite theory although I favoured their transport inside the symbiotic cells and not as Nasu has shown, on their surfaces. Nasu's profound experience of the morphology and embryology of cicadellids forms the basis of a most satisfying piece of work.

Papers by Shikata and Maramorosch, and Maramorosch, Shikata and Granados, beautifully illustrate the uses of fine sectioning techniques in investigating the distribution and behaviour of spherical particles of wound tumour and rice dwarf viruses, and the aphid-transmitted pea enation mosaic virus. Viruses with flexible, rod-shaped particles (Brakke *q.v.*) seem never to be propagative and so have not been seen in tissues of insects. No illustration of short-rod, or bacilliform particles is given, but fine-sectioning is largely responsible for the detection and investigation of these also.

Nonpropagative Leafhopper borne Viruses, by Ling, introduces a new problem of nomenclature, not concerned with the status of the pathogen (as with the 'Yellows' viruses), but with its behaviour in relation to the vectors. Rice tungro virus was at first said to be nonpersistent, but its behaviour seems to resemble that of beet yellows virus in being semi-persistent and noncirculative. Contrary to what the title implies it could still be propagative, because some beetle-transmitted viruses accumulate in the gut, and might multiply in the cells of the lining wall. If this occurred in the fore-gut which is cast during ecdysis, it would explain the partial persistence of semi-persistent viruses and their failure to be transmitted transstadially. This could not be true of beet curly-top virus which is circulative, and the evidence that it is not propagative is tenuous. With many persistent plant viruses especially those transmitted by aphids, e.g. potato leaf roll and pea enation mosaic (Sylvester *q.v.*) and also insect pathogenic viruses such as bee paralysis virus (Bailey *J. Invert. Path.*, **7**, 1965) the initial 'charge' of virus acquired determines the extent of multiplication and or persistence in the vector. Its effective persistence places curly-top firmly with the persistent hopper-transmitted viruses; it is surely circulative, but we cannot be certain whether it is propagative or not. The negative evidence for its multiplication in the vector adduced by Freitag in 1939, although original and interesting *per se*, is not a valid criterion.

These two viruses illustrate the confusion that exists in the present use of terms to define different kinds of vector-transmission. Persistent, nonpersistent and semipersistent (Watson and Roberts, *q.v.*, 1940, Sylvester, *q.v.*, 1962) are empirical, but have, as Medawar (The Art of the Soluble, 1967) has said of certain other antithetic pairs (antigen and antibody, male and female), 'matching oppositeness in common . . . that is not the taxonomic key to some other deeper affinities'. Kennedy *et al.*, suggested 'Stylet-borne, circulative and circulative-propagative' as better alternatives. These are not opposite in sense, and have no flexibility in respect of intermediate forms. Unlike persistence they are difficult to establish and are never even looked for until other properties have been defined. Probably only about half the viruses have actually been shown to possess attributes that are ascribed to them mainly because of their persistence. Tungro virus was at first described as stylet-borne, only because it could not be defined as circulative or propagative.

We can be reasonably sure that all nonpersistent viruses are carried around or within the mouthparts as Hoggan suggested in 1933, but we cannot be sure, as Pirone (*q.v.*) is, that all are carried on the outside surfaces of the last 15 microns of the stylets (Bradley and Ganong, *q.v.*, 1955). We do not know if the cause of their specificity of transmission is electrostatic, behavioural, biochemical or a combination of these, or something else we have not yet thought of.

Some of these considerations are discussed by Sylvester in his 'Viewpoint' on aphid-transmission. He considers contradictory evidence for strawberry crinkle and cauliflower mosaic being stylet-borne as defined by Pirone, and emphasizes the propagative nature of persistent viruses, potato leaf roll and pea enation mosaic.

Pirone's important contribution to our knowledge of the transmission of nonpersistent viruses is to show that at least those with spherical particles (cucumber mosaic) and bacilliform particles (lucerne mosaic) can be transmitted from purified preparation by making aphids probe into them through membranes. It was not for want of trying that this had not succeeded previously, but all attempts had been made with the largest group, having long flexible particles, and these have not yet been transmitted by such methods. Pirone has failed to transmit tobacco mosaic virus in this way from highly concentrated preparations, although it is acquired, and subsequently released into feeding media. He suggests that this failure may have such causes as the inhibitory action of aphids' saliva on virus-infectivity or plant-susceptibility, or aphids failing to probe 'susceptible sites'. However, Teakle and Sylvester, 1962, found that tobacco mosaic sprayed onto leaves could be transmitted by aphid-probing. Therefore the probing sites are suitable and the saliva ejected during or after probing does not prevent infection.

Nishi shows that TMV can be inhibited by a component of saliva collected while feeding aphids on artificial media. Turnip mosaic, a non-persistent flexuous-rod type virus, is also inhibited, but relatively more slowly than tobacco mosaic. However, the inibition of TMV, judged from lesion counts on manually inoculated plants, is never complete and its concentration in plant cells and purified preparations is very much greater than that of cucumber mosaic. The idea of such inhibition by saliva has long been mooted, but never accepted because of the great superiority of TMV in quantity, stability and infectivity. If TMV were only occasionally transmitted it might be true, in the light of Nishi's results, but complete failure is still unexplained.

Swenson describes factors affecting plant-susceptibility to non-persistent viruses, predictably similar to those that affect manual inoculation. Most of such results are evaluated on the hypothesis that local lesion formation and the infections, individual or multiple, caused by probing aphids are local and independent. Swenson attributes this to Bindra and Sylvester, 1961, although both the hypothesis and the statistical methods used to test it, have been known for many years. Perhaps the aphorism that 'Science advances by rediscovering the same things every 25 years' has some truth.

Emerging from these controversies, it is shattering to read in Rochow's opening lines that 'Less is known about circulative (persistent) viruses than about stylet-borne ones'. This, roughly interpreted, means that after 40 years of investigation we know little about aphid-transmission at all. Rochow, however, underestimates the effect of his own development of artificial feeding techniques for bioassay of persistent aphid-transmitted viruses, also the electron microscopy of fine-sections, the use of constant environment in exactly determining the factors affecting transmission, virus purification, aphid-to-aphid injection, and other techniques that have helped us to interpret the behaviour of persistent viruses. Few of these new techniques seem to have helped much with the nonpersistent ones. Even now we lack the ability to measure, quantitatively, virus uptake (or acquisition if these are different) by aphids during probing; nor can we detect its position objectively by electron microscopy. Until there is objective, instead of, as at present, largely circumstantial evidence, there is bound to be some uncertainty.

One object of *Viruses, Vectors and Vegetation*, as a 'stimulating Forum for discussion' (Preface *q.v.*) seems to be fulfilled if this, much longer review than I intended, is any evidence. But that Forum is a very large and complicated place, you may have to run about a lot to get anywhere. The book will almost certainly become a classic, and although it is perhaps already a little more classical than was originally intended, will be a valuable source of reference and information.