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with locusts in six different territories during twenty-six out of twenty-eight successive months, and sprayed during twenty-four of these months (F.A.O., 1959; Rainey, 1956). The exploitation of the full potentialities of the control methods and resources which are now available against the Desert Locust has thus become a problem, above all, of operational research on an international scale. It is therefore encouraging that in the new Desert Locust Project, begun this month by F.A.O. with the financial support of nineteen governments and of the United Nations Special Fund, operational research appears with appropriate prominence.

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Discussion

Mr. Q. A. Geering asked Dr. Rainey for an explanation of the way in which the aircraft spray runs were made in relation to the layout of the flying locust swarm. Dr. Rainey replied that the pilot of the plane selected a straight path across the top of the visually densest part of the swarm, and that this was done afresh for each run-in; as a swarm consisted of many groups of locusts, with the widest possible diversity of orientation between groups, each run-in, or spray-line, was effectively independent of those made before it, for the swarm could be regarded as re-randomising itself, while the plane was turning for the next run.

Dr. A. P. Arnason enquired whether crops had to be protected from spray-damage during such operations. Dr. Rainey said that this was not often a serious problem, since much of the control of swarms from the air was carried out in regions remote from cultivated areas. When spraying swarms over crops had been unavoidable, a minimum spraying height, usually 200 feet, had been specified from experimental data. There had, however, been one such occasion when large drops of DNC, due to temporarily defective jets on particular aircraft, had damaged sisal in Tanganyika; and the use of BHC had, on occasion, caused tainting on tea and on grass used for grazing.

Mr. T. Greaves asked, in view of Dr. Rainey's remarks that the swarm re-orientated itself after the passage of the plane, what immediate effect insecticides had on the locusts. The *immediate* effect was negligible, replied Dr. Rainey, even when DNC was employed, though with this insecticide half of the locusts killed by a particular operation could drop out of a travelling swarm within an hour of spraying. With less rapid materials, a corresponding stage would perhaps not be reached for twenty-four hours, and careful ground observations were needed to give accurate data on the effectiveness of such spraying.

Mr. L. P. Lefkovitch asked whether an opinion could be expressed on the effect on the total fauna of the use of dieldrin sprays over large areas, and whether any research was being carried out to elucidate such effects. Dr. Rainey said that no such work with dieldrin was known to him, but work on these lines had been carried out on such effects of the use of

large quantities of BHC concentrates against swarms in Morocco, where the effects on the other insect fauna were said to be striking but not long-lasting.

DISCUSSION ON DEVELOPMENTS IN THE STUDY OF PLANT VIRUSES AND THEIR VECTORS, AND THEIR BEARING ON CONTROL MEASURES*

Chairman: Mr. F. C. Bawden, *Director, Rothamsted Experimental Station*

The Chairman opened the meeting by remarking that the transmission of fungal diseases by insects would have been an ideal subject for this first joint session of the Seventh Commonwealth Entomological Conference with the Sixth Commonwealth Mycological Conference, but unfortunately there were few people who could contribute to such a topic, and therefore viruses were the next best thing. Five years ago the title would have said " insect vectors," and recent advances to incriminate other animals were significant.

The Ways in which Plant Viruses are Transmitted by Vectors

By Dr. M. A. Watson

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Examples of plant viruses, grouped according to their vectors and the ways in which they are transmitted, are shown in the Table below, but it contains a lot of speculation, and will probably soon be out of date. The much abused terms, persistent and non-persistent, at least have definitive meaning but much of the rest is speculative, and I have had to make some enlightened guesses so as to include a reasonably representative collection of examples. However, the Table may serve some useful purpose if only as an aid to remembering the increasing variety of Invertebrate-transmitted viruses and their interactions with their vectors. This kind of information is not only necessary to those single-minded enthusiasts who worry about mechanisms of transmission but to all who are concerned with crop growth and food production, for the way in which a plant virus is transmitted determines how it spreads in crops and the kind of control measures that are effective against it. Also, grouping the viruses according to kinds of transmission emphasizes other similarities that help in diagnosis or investigation of new and unfamiliar diseases. Note the use of the expression " Invertebrate-transmitted." Up till recently we have been able to use " Arthropod-transmitted " as a collective adjective, but the discovery of nematodes as vectors of plant viruses compels the use of the more general term.

The three criteria I have used to distinguish the different kinds of transmission are: first the latent or incubation period, second the persistence of infectivity of the vectors, and third the passage of virus through the moult. The *incubation or latent* period is an interval between the acquisition of virus by a vector and the time when it is able to initiate infection in a healthy plant.

Persistence is the time for which a vector can go on infecting healthy plants after it leaves the infected ones. Viruses in Group I, for example, Henbane mosaic, hardly persist at all, hence the term non-persistent. Those of Group II, for example, Beet yellows, may persist for two or three days, Barley yellow dwarf, in Group IV, persists for two or three weeks, and striate mosaic for two or three months. Vectors of the last two sometimes do not infect the first plants they feed on, because of the delay period.

The third criterion, *passage of virus through the moult*, is based on whether or not an infective immature vector can go on causing infection after it has moulted and developed into a more mature form. All the vectors of plant viruses grow by sloughing off their exoskeleton when it becomes too small for them. The cast-off material or *exuvium* includes the chitinous skin and mouth parts and tissues derived from the embryonic ectoderm, the fore and hind gut, trachaeae and so on. All these are replaced each time before the old ones are discarded. Emergence from the egg is a special sort of ecdysis, so passage of a virus through the egg can be considered in the same category as that through the moult.

* Joint meeting with the Sixth Commonwealth Mycological Conference

EXAMPLES OF VIRUSES GROUPED ACCORDING TO THE WAYS IN WHICH THEY ARE TRANSMITTED BY VECTORS

Groups	Vectors	Examples	Latent or Incubation period	Passage through moult	Persistence in feeding vectors
NON-PERSISTENT	TRANSPORT. EXTERNAL—PASSIVE—PROBABLY CARRIED ON EXUVIAE				
I	APHIDS	Henbane mosaic† Potato virus Y† Cucumber mosaic† Beet mosaic† Cabbage black ring spot† Cauliflower mosaic†	None	None	½ to 2 hrs.
PERSISTENT II	MEALYBUGS	Swollen shoot	None or very short	None	From a few hours to 3 or 4 days
	APHIDS	Beet yellows* Raspberry viruses* Strawberry mottle			
	MITES	Ryegrass mosaic†			
	TRANSPORT. INTERNAL—PASSIVE—OFTEN RECOVERABLE FROM THE BLOOD				
III	BITING INSECTS	Squash mosaic† Turnip yellow mosaic†	None or short	Not known: not through metamorphosis	Days to months often depending on quantity of virus acquired by vectors
IV	APHIDS	Barley yellow dwarf Carrot motley dwarf* Strawberry yellow edge Groundnut rosette	4–20 hrs.	Through the moult but not through eggs	
	WHITE FLIES (Aleurodidae)	*Bhendi* yellow vein Cotton leaf curl	6–8 hrs. 4–20 hrs.		
	CICADELLIDS	Beet curly top Maize streak	3–20 hrs. 12–30 hrs.		
V	MITES	Wheat streak mosaic†	Not known		
	THRIPS	Tomato spotted wilt†	5–9 days		
	NEMATODES	Grape fan-leaf† Arabis mosaic†	Not known		
	TRANSPORT. INTERNAL—WITH MULTIPLICATION				
VIa	APHIDS	Potato leaf roll	12–30 hrs.		
VIb	CICADELLIDS	Aster yellows Peach yellow leafroll	10–30 days		Usually months: not obviously dependent on quantity of virus acquired
VIIa	CICADELLIDS	Wound tumour Potato yellow dwarf† Green petal Clover witch's broom	10–30 days 4–8 weeks	Transmission through eggs infrequent	
VIIb	CICADELLIDS	Rice dwarf Clover club leaf	10–30 days	Transmission through eggs frequent	
	DELPHACIDS	Rice stripe Wheat striate mosaic	7–30 days		

* Manually transmitted with some difficulty.
† Easily manually transmitted.

An example of Group I is henbane mosaic (HMV), a non-persistent virus affecting solanaceous plants used for drugs. It is transmitted by the Aphid, *Myzus persicae* (Sulz.). When tobacco plants are fed on by Aphids that have been starved and then fed for either two minutes or twenty-four hours on plants infected with HMV, those fed for twenty-four hours infect many fewer plants than those fed for two minutes (Watson and Roberts, 1939). This is an easily repeatable result so long as the feeding times given on the infected plants are really short. The optimum is between one and two minutes. When Aphids are left on the plants for even five minutes their infectivity is already lowered, and after one hour it is minimal.

Beet mosaic (BMV) is another non-persistent virus and it is interesting to compare its behaviour with that of beet yellows virus. Both are transmitted to sugar beet by *M. persicae*. BMV was best transmitted when the Aphids were starved and then given two minutes feeding on infected leaves. Unstarved Aphids were poor vectors after two minutes feeding, but did better after feeding a long time. However starving made no difference to transmission of beet yellows. Aphids that had fed for fewer than five or ten minutes on infected leaves did not transmit but they did so after longer times, and their efficiency increased with increasing feeding times up to about eight hours (Watson, 1946).

Non-persistent viruses, such as henbane mosaic and beet mosaic, are not only very rapidly acquired but also rapidly transmitted, the whole process taking only a few minutes, but they are lost within an hour when the Aphids feed on healthy plants. Beet yellows is slowly acquired and slowly transmitted, but Aphids may go on transmitting it for two or three days. When Aphids migrate into a sugar beet crop they often move about quickly at first and so transmit beet mosaic, but the virus must come from a nearby source, otherwise the vector would lose it on the way to the crop.

Beet yellows need not come from a nearby source, but its vector must feed for several hours on an infected plant to transmit it efficiently. When it is brought from a distance, infective Aphids are likely to be few and infect few plants, but these plants become foci of infection from which virus spreads while the Aphids are building up their summer infestation.

The actual mechanisms of transmission of these two kinds of viruses (Group I and Group II) are still very uncertain. The non-persistent viruses are so rapidly transmitted that they can do little else but adhere in some way to the mouthparts. Experiments have shown that they are probably carried on the extreme tips of the stylets (Bradley and Ganong, 1955). It has been suggested that they enter grooves, or get wedged behind scales or bristles on the chitinous surfaces of the stylets (van Hoof, 1958). If so, it is difficult to understand how different non-persistent viruses are specifically transmitted by different species of Aphids, and conversely, why very contagious viruses like tobacco mosaic and potato virus X are not transmitted in the same way. Even serologically related strains of non-persistent viruses may vary in their ability to be transmitted by different species of Aphids. Potato virus Y is readily transmissible by *M. persicae* but potato virus C is not, cucumber mosaic has many aphid vectors, including *M. persicae*, but its related strain from spinach is transmissible, apparently, only by *Aphis gossypii* Glov., and *Myzus ascalonicus* Doncaster (Badami, 1958).

Beet yellows mosaic is much less stable *in vitro* than beet mosaic, and yet it lasts much longer in the insect. Presumably it is carried on or in some tissue where it is protected from inactivation better than in plant sap.

As the Group II kind of viruses do not pass through the moult, they may be harboured in the insects on some part of the exuvium that is biologically active only between moults. At present there is no relevant information.

The viruses of Group III, transmitted by biting insects, are very stable *in vitro* and have had much interesting work done on them which does not concern us here. They may be transmitted by grasshoppers and possibly by Aphids, but their behaviour in these has not been studied. In beetles they survive for long periods in the alimentary canal and in the blood. They are probably injected into healthy plants by regurgitation. Freitag (1956) has said that Squash mosaic cannot survive pupation although both larvae and adults can acquire and transmit it. In the pupae of holometabolous insects nearly all the tissues break down and are re-organised. Probably the virus is destroyed by enzymes or discarded with the waste products. Perhaps that is why few plant viruses are transmitted by vectors with complete metamorphosis.

Barley yellow dwarf is an example of a Group IV virus. It has a short incubation period in its aphid vector, but long persistence. The cereal diseases caused by it are of great economic importance in many countries. Barley yellow dwarf is even more slowly acquired and transmitted than beet yellows virus. Perhaps ten per cent. of the Aphids can pick up some virus when fed on infected leaves for about two hours, but usually they will not transmit until they have fed on healthy plants for several hours more.

Aphids that feed on infected plants for a day are much more likely to infect than those fed for shorter times, and need less time on healthy plants. It is difficult to be critical about these times because they affect each other. The slowness of transmission may be because Aphids take a long time to acquire virus, or because they acquire so little that it takes a long time to reach the healthy plants, or because virus has been acquired but takes some time to pass from the alimentary canal to the salivary glands, which would in effect be the simplest kind of incubation period, and is usually accepted as such. All these factors would cause apparent delay between the Aphids having access to virus and being able to infect plants. As they are correlated it is impossible at present to measure their relative importance.

Other things could happen to the virus in the vectors as well as moving to the salivary glands, and one of these could be multiplication in the tissues of the vectors. We know that several hopper-transmitted viruses multiply in their vectors, and it has also been demonstrated that potato leaf roll virus does. But for this fact I would have included leaf roll virus in Group IV, because it is so like the others of that group. One is tempted to say that if leaf roll can multiply in its vectors so could yellow dwarf and carrot motley dwarf viruses also. However, if they do so it does not affect the efficiency with which they are transmitted. This is illustrated by the following results:—Aphids were fed on oats infected with yellow dwarf virus, and leaf hoppers on sugar beet infected with curly top virus, for one hour and for twenty-four hours. They were then removed to fresh healthy plants every day, until the Aphids had fed on twenty plants and the hoppers on 100 (Hoppers, of course, live much longer than Aphids). When fed for one hour on infected plants each Aphid infected " only one or two plants " out of the twenty fed on and the hoppers infected four, but when fed for twenty-four hours the Aphids infected fourteen plants and the hoppers infected twenty. The figures are taken from the work of Freitag (1936) and Rochow (1959). So the time of feeding on infected plants determined the amount of virus transmitted. This is true also of potato leaf roll virus (Heinze, 1959), although leaf roll is reported to multiply in its vectors (Stegwee and Ponsen, 1958). Multiplication would be expected to make transmission independent of the quantity of virus imbibed, as it does for wheat striate mosaic and some other leaf-hopper-transmitted viruses, but apparently it does not do so in Aphids. Perhaps the truth is that transmission of some plant viruses is only incidental to their behaviour in the vectors.

The next group is Group V. This contains a motley assemblage that probably have nothing to do with each other. Dr. Broadbent will mention spotted wilt virus, and Dr. Posnette will tell you about the nematode transmitted viruses, so I will quickly pass over them.

There is quite a wide variety of behaviour among the hopper-transmitted viruses in Groups VI and VII. Wheat striate mosaic provides examples of most, with some extra complications of its own. It is transmitted by *Delphacodes pellucida* F. and the symptoms it causes in wheat plants vary from fine broken chlorotic streaks to severe generalised chlorosis resembling that sometimes seen in genetic chimaeras. The plant-hoppers can pick up the virus from infected leaves in two or three hours and transmit in about half-an-hour, but they need at least a week to do both. Prolonging the times of feeding on infected and healthy plants increases the numbers of hoppers that acquire virus, but does not increase the infectivity of individual hoppers. Their efficiency depends very largely on their parentage, for different races vary enormously in their ability to acquire and transmit virus. Some are so poor that only occasional individuals will occasionally transmit; others are so efficient that almost all can become able to transmit constantly for months (Slykhuis and Watson, 1958).

D. pellucida exists in several races that vary in their ability to transmit wheat striate mosaic. When three groups of individuals from each of three races of hoppers were given

equal opportunities to infect wheat seedlings, race A infected nine, race B twenty-nine and race C fifty-one plants. The incubation periods of the virus in the vectors also vary in the different races. Sixteen of race C, three of race B and none of race A infected within ten days of leaving the infected plants. In other words, race C infected much more quickly than the other races, because its incubation period was shorter.

Vectors of beet yellows, barley yellow dwarf and wheat striate mosaic lose infectivity at different rates when feeding on healthy plants. Beet yellows is optimally transmitted within a few hours, but is lost from the infective vectors within about seventy hours. Yellow dwarf starts to be transmitted at once provided the vectors have fed longer than a few hours on infected plants. The Aphids transmit highly efficiently for about a week, but then begin to fail with increasing frequency. Some completely lose the ability to infect. This suggests that their virus content is quantitatively limited.

Vectors of wheat striate mosaic virus do not transmit until at least a week after they acquire virus. Then the numbers of plants infected each day increase slowly, reflecting the different lengths of incubation periods by hoppers of varying vector-efficiency. Once a hopper becomes infective its efficiency depends mainly on its race and very little on its opportunity for acquiring virus.

Not only do the individuals of efficient races maintain a sufficient store of striate mosaic virus to infect plants for the rest of their lives, but they also hand it on to their offspring. And the offspring hand it on to their offspring, and so on, apparently *ad infinitum*, or at least for a great many generations. This behaviour has been used by Fukushi with rice dwarf virus and Black, for clover club leaf virus, to prove that plant viruses can multiply in the tissues of insects. Virus could be inherited through so many generations without renewal that there was no other possibility.

With striate mosaic not only are the young hoppers born infective, but the virus injures many of the embryos so that they fail to hatch. The embryos develop almost to the stage of emergence but then many of them collapse and die. Those that do emerge can usually infect plants as soon as they are hatched (Watson and Sinha, 1959). This means that really efficient races, if they acquire virus, are not able to breed as rapidly as less efficient or virus free individuals. Their progeny may be reduced to a half, or even to a quarter. So the better able they are to infect plants, the less likely they are to survive in nature. This is probably one reason why the virus does not spread rapidly in the field, even when the vectors are plentiful.

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