VARIATION WITHIN AND AMONG APHID VECTORS OF PLANT VIRUSES *

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INTRODUCTION

In an early review on insect vectors, K. M. Smith (1931) wrote: "The question of the relationship of strains, biological races, and varieties of insect vectors in regard to their ability to transmit viruses is a subject of great interest and one which up to the present has been much neglected." This statement seems generally appropriate today despite the passage of 30 years. The existence of vector variations has often been considered and such variations have been used to explain anomalous results, but relatively little attention has been given to thorough studies of the variations or of the contributions that an understanding of them might make to basic questions of virus-vector relationships.

Perhaps more is known about variations within and among leafhoppers than any other group of vectors. The classical work of H. H. Storey and more recent experiments by L. M. Black and his associates have made major contributions in demonstrating the importance of variations among individuals of races of one leafhopper species, the role played by the gut wall in some instances of specificity, the inter-relationships between virus strains and leafhopper species, the role of leafhopper hereditary mechanisms, and other aspects of leafhopper variation. Since most of the leafhopper work has been reviewed recently (Black, 1953, 1962; Day, 1957; Maramorosch, 1960; Smith, 1957), it will not be treated here.

Some information is available on variation within or among other plant virus vectors, such as bugs, thrips, and mites; but attention will be restricted here to aphids, a group whose variation has received considerable recent attention. Aphid transmission of plant viruses is characterized by a wide range of mechanisms by

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which transmissions seem to occur (Sylvester, 1962). The mechanisms at one extreme include those, usually termed nonpersistent or mechanical, in which aphids can acquire and transmit virus within seconds or minutes, but soon lose the ability to transmit virus unless they have access to another virus source. At the other extreme are mechanisms usually called persistent or nonmechanical. In persistent transmission, aphids often require hours for acquisition and transmission, but they can continue to transmit virus for many days after removal from the virus source and transmission continues even after a molt in many cases.

It is the purpose of this paper to give some illustrations of the kinds of variation that occur within and among aphid species that transmit plant viruses and to consider in more detail one of the most recently discovered examples of variation.

VARIATION WITHIN ONE APHID SPECIES

Three kinds of variation within an aphid species have been described. These include variations in virus transmission among different clones or strains of one species, among various developmental stages, and among different forms of one species. As Stubbs (1955) pointed out, it is surprising that variability among aphids had received so little early attention. Most reports on variation within one aphid species have appeared within the last 10 years. The polymorphism of aphids, their capacity for both parthenogenetic and sexual reproduction, and the production of many generations in a short time seem to make them particularly suspect in regard to variations in virus transmission and particularly suitable for use in studies of the variations.

Most investigators apparently have realized the possible importance of variation within one aphid species. For example, Hoggan (1929) used three different clones of *Myzus persicae* (Sulzer) in early studies on transmission of cucumber mosaic and tobacco mosaic viruses. Hoggan's failure to find any evidence for variability among the three clones seems to be the general experience of many workers. The scarcity of reports on variations within an aphid species could indicate that such variations are less common than might be expected or that the variations have often been overlooked.

Aphid Clones

Despite the long realization that aphid clones might differ in their ability to transmit viruses, the report by Stubbs (1955) is one

of the first demonstrations of the variation and one of the first reports to emphasize its possible importance. Stubbs (1955) found that different cultures of *M. persicae* varied in ability to transmit (persistently) a yellows virus from spinach. The aphid cultures remained active or inactive with respect to virus transmission in successive experiments.

Björling and Ossiannilsson (1958) made extensive studies involving about 100 strains and six aphid species in the transmission of two viruses which also had a persistent relationship with the vectors. Differences in transmission efficiencies were found for *M. persicae, Aphis fabae* Scopoli, and *Myzus ascalonicus* Doncaster. These workers were able to group 85 strains of *M. persicae* in a series ranging from those in which 10 per cent transmitted to those in which 80 per cent of the aphids transmitted beet yellows virus. More of the strains fell into the 40-50 per cent group than in any other category. Ability of the aphid strains to transmit was not related to the plant species on which the aphid was originally found. The relative differences in ability to transmit both beet yellows virus and potato leaf roll virus were of the same order for two clones of *M. persicae*. Crosses between different clones of *M. persicae* were used to obtain evidence for the genetic basis for the variation. Additional evidence for variability among clones of *M. persicae* in the transmission of potato leaf roll virus was reported by Williams and Ross (1957), but Day (1955) was unable to isolate clones of *M. persicae* that differed in transmission of this virus.

Variation among clones of a different aphid species was reported by Rochow (1960*a*). When collections of greenbugs (*Toxoptera graminum* Rondani) from Florida, Wisconsin, and Illinois were compared as vectors in the persistent transmission of several isolates of barley yellow dwarf virus, those from Wisconsin and Illinois were found to transmit the virus fairly efficiently, but the collection from Florida was virtually inactive as a vector of the virus. Although morphological differences have generally not been observed among clones that vary in their ability to transmit viruses, the inactive clone of *T. graminum* had a beak tip slightly different from that of the two active clones (Rochow, 1960*a*).

When Frazier (1960) compared two clones of *Pentatrichopus fragaefolii* (Cockerell), he found one capable of transmitting all four strains of strawberry veinbanding virus tested, but a second clone transmitted only three of the four strains. The second clone was distinct morphologically, and although Frazier considered it an atypical *P. fragaefolii,* he pointed out that it might represent a variety of any one of three aphid species.

The work of Simons (1959) shows that variation among clones is not restricted to aphid-virus combinations having persistent transmission. Clones of the cotton aphid (*Aphis gossypii* Glover) differed in the nonpersistent transmission of southern cucumber mosaic virus over a period of several years. The relative transmission of the clones was not affected by changing the plant species used as virus source, but changing the aphid host plant did slightly affect transmission efficiency of the clones. An important result of the studies by Simons (1959) is the demonstration that an aphid clone efficient in transmitting one virus will not necessarily be efficient in transmitting another virus. Differences among clones in transmission of southern cucumber mosaic virus did not occur in parallel tests on the transmission of potato virus Y.

Consideration of variation among aphid clones has usually been directed toward individuals or clones that are unable to transmit virus in contrast to most individuals of a species that are good vectors. The possible importance of the opposite emphasis, that is, occurrence of relatively few individuals of a species that can transmit virus, was pointed out by Bawden and Kassanis (1947). They suggested that only occasional individuals of *M. Persicae* might be vectors of potato virus C in contrast to most individuals of this species which are unable to transmit the virus.

In addition to variation among clones of an aphid species in regard to virus transmission, other types of aphid physiological specialization are known. For example, Dahms (1948) noted differences among collections of *T. graminum* in the damage caused to certain small grain varieties, and Shirck (1960) found differences among strains of *M. persicae* in response to malathion.

Aphid Stages

Differences among developmental stages of insects in the transmission of plant viruses are particularly striking for thrips, a subject recently reviewed by Sakimura (1962). Some reports indicate that quantitative variations may occur among developmental stages of an aphid species.

In studies on the persistent transmission of filaree red leaf virus, Anderson (1951) noted that young nymphs of *Macrosiphum geranicola* (Hille Ris Lambers) seemed to acquire the virus more readily than did adults; the minimum latent period was shorter in nymphs than in adults. Another example is the finding (Simons, 1954) that first instar nymphs of the pea aphid (*Macrosiphum pisi* Kaltenbach) were more efficient vectors of pea enation

mosaic virus than were adult aphids and that this virus had a shorter latent period in the nymphs than in the adults. Simons considered this a possible reflection of differences in vector efficiency of nymphs and adults.

Aphid Forms

The occurrence of more than one form is characteristic of the life cycles of many aphids. For example, winged viviparous females that are common during the summer often transmit viruses in the field, but wingless viviparae are usually used in experimental studies. Sexual forms, either winged or wingless, play important roles in nature. Demonstration of variation in virus transmission among such different forms of one species has been another recent development.

Paine and Legg (1933) reported a case in which one aphid form transmitted virus but another did not. They obtained transmission of hop mosaic virus by the spring-winged form of *Phorodon humuli* (Schrank), but not by the summer-wingless form. Orlob and Arny (1960) found oviparae and fundatrigeniae of *Rhopalosiphum fitchii* (Sanderson) to be capable of transmitting barley yellow dwarf virus but four other forms of the same species failed to transmit the virus. More recently Orlob (1962) tested various forms of four aphid species as vectors of potato virus Y and cabbage virus B. Oviparous females of *Macrosiphum euphorbiae* (Thomas) and *Brevicoryne brassicae* (L.) transmitted both viruses as efficiently as did apterous viviparous females. A difference among forms of *Aphis nasturti* (Kaltenbach) in the transmission of potato virus Y was detected. Potato virus Y was transmitted by the migratory forms such as gynoparae, males, and fundatrigeniae, which spend part of their life-cycle on virus-susceptible hosts; no transmission was obtained by oviparae and fundatrices, which spend their entire life-cycle on the winter hosts. In this instance, the variation among aphid forms seemed to be related to the host plant of the aphid form.

VARIATION AMONG APHID SPECIES

The variation in ability of different aphid species to transmit plant viruses covers a wide spectrum. It includes variations among species in transmission efficiency. In one thorough study on efficiency, for example, Bradley and Rideout (1953) found that the relative efficiencies of *Myzus persicae, Aphis abbreviata* Patch, *Macrosiphum solanifolii* (Ashmeade), and *Myzus solani*(Kaltenbach)

in the transmission of potato virus Y were 55, 31, 9, and 4, respectively. Little is known about the basis for such quantitative variations, but Bradley and Rideout found that efficiencies of these four species were not due to feeding behavior.

Another aspect of variation among aphid species involves the problem of why one species is a vector of a particular virus while another species is not. Attention will be centered here on consideration of two recent examples that appear to fall in this general category. On the surface, such variations seem to involve qualitative rather than quantitative differences, but this apparent distinction may not be real. One of the variations to be considered here involves a nonpersistent aphid-virus relationship; the other deals with persistent transmission.

The nonpersistent example was described by Badami (1958). A strain of cucumber mosaic virus, which had been isolated originally from spinach, was readily transmitted by *M. persicae* initially, but lost this property during transfers in the greenhouse. The strain which was no longer transmitted by M. *persicae,* however, remained transmissible by *Aphis gossypi* and *Myzus ascalonicus;* at the same time *M. persicae* remained a good vector of other strains of cucumber mosaic virus. In other words, an isolate of cucumber mosaic virus was transmissible by *M. ascalonicus* and *A. gossypi* but not by *M. persicae,* which was an efficient vector of other isolates of the same virus. Several lines of evidence indicated that the basis for this type of vector specificity involved a change in the virus and not in the vector (Badami, 1958).

A second example of variation among aphid species involves the persistent transmission of barley yellow dwarf virus. The remarkable specialization among isolates of this virus and some of the aphid species that transmit it has been encountered in several laboratories in recent years. The variation has been treated briefly in general reviews by Bruehl (1961) and Rochow (1961*a*), but it will be discussed more fully in the following section.

Vector Specificity of Barley Yellow Dwarf Virus

Introduction. Five aphid species were shown to be vectors of barley yellow dwarf virus, and the aphid-virus relationship was found to be persistent in the original studies on the disease by Oswald and Houston (1953). Additional aphid vectors have since been described. Although careful comparisons of the transmission efficiencies of the different aphid species had not been made, most workers generally found *Rhopalosiphum padi* (L.) to be the most efficient vector; this species was the only one used in many early

studies. (*R. padi* has also been identified as *R. fitchii* (Sanderson) and *R. prunifoliae* (Fitch) by some workers—for uniformity, only the name *R. padi* will be used here.) For example, Toko and Bruehl (1956) noted 98.7 per cent transmission by *R. padi* and 40.5 per cent transmission by *Macrosiphum granarium* (Kirby) in one comparison of two aphid species.

A more striking difference between *R. padi* and *M. granarium* was first noted by Toko and Bruehl (1957, 1959) when they tested 34 field collections in Washington. They found that barley yellow dwarf virus was transmitted from 32 of the collections by both aphid species, but that it was transmitted from one collection only by *R. padi* and from another collection only by *M. granarium*. A similar variation between these two species was found in New York (Rochow, 1958a), but the occurrence of virus transmitted from field samples only by *M. granarium* and not by *R. padi* was common, not rare, as in Washington. Similar variations in transmission of the virus have been encountered in Canada (Slykhuis *et al.*, 1959; Smith, 1961), in Great Britain (Watson and Mulligan, 1960), and in other regions.

A further variation was encountered when barley yellow dwarf virus was recovered by means of *Rhopalosiphum maidis* (Fitch) in 1959, 1960, and 1961 from a few field samples from which virus was not transmitted by *R. padi* or *M. granarium* (Rochow, 1959c, 1960*b*). Direct comparisons of three aphid species and different isolates of barley yellow dwarf virus have shown the existence of at least three vector-specific strains of the virus (Rochow, 1961*b*). One strain (MGV) is transmitted efficiently by *M. granarium* but not transmitted regularly by *R. padi* or *R. maidis*. A second strain (RPV) is transmitted efficiently by *R. padi* but not transmitted regularly by *M. granarium* or *R. maidis*. The third strain (RMV) is transmitted fairly efficiently by R. *maidis* but not transmitted regularly by *M. granarium* or *R. padi*. Although minor differences sometimes occur in severity of symptoms caused by the three virus strains, the differences have not been consistent enough for reliable differentiation among the vector-specific strains I have studied.

Since most of the studies on vector specificity of barley yellow dwarf virus have involved *R. padi* and *M. granarium*, further discussion of this system will be restricted to these two species and the virus strains they transmit.

Methods available. Barley yellow dwarf virus offers several advantages in studies on mechanisms of persistent aphid transmission and on variation among aphid species. If the proper virus isolate and the proper aphid species are used, virus transmission

is very efficient. Oats serve as an excellent test plant because many varieties develop clear symptoms in the greenhouse, usually within two weeks after inoculation. Both *R. padi* and *M. granarium* are easily reared on barley or other hosts, although special precautions are needed to keep colonies free of barley yellow dwarf virus because no good aphid hosts immune from the virus have been found (Rochow, 1959*b*). The main advantages for studies of this aphid-virus system result from availability of two specialized techniques that make possible many kinds of experiments not available for other aphid-virus combinations.

The first technique is transmission of barley yellow dwarf virus acquired from liquid extracts by aphids feeding through membranes (Rochow, 1960c). This technique is used regularly in our laboratory to assay partially purified virus preparations and in certain aspects of studies on vector specificity. Although it was useful initially only for *M. granarium* and the virus isolates transmitted by this species, recent studies (E-Wa Pang, unpublished) indicate that the technique can be used also for *R. padi*. It provides a relatively simple qualitative test for barley yellow dwarf virus in liquid preparations.

The membrane-feeding technique is carried out by placing aphids that have been starved for several hours into a small feeding chamber. Each feeding chamber is topped with an animal-capping skin membrane previously fastened over the end of a glass tube. The liquid preparation to be tested is placed in the glass tube so that the aphids are able to feed through the membrane top of the feeding chamber into the test solution above it in the tube. Following an acqusition feeding period of about 18 hours at 15° C., the glass tubes are removed from the feeding cage and the aphids are transferred to test plants (FIGURE 1).

The second technique for basic studies with barley yellow dwarf virus is the needle-injection method used so successfully in other insect-virus studies (Maramorosch, 1959). Many insect-virus systems are known in which a plant virus can be transmitted from insect to insect by needle injection. An indication of the usefulness of the injection technique for studies with barley yellow dwarf virus is that virus can also be transmitted readily from infected plants to aphids (Mueller and Rochow, 1961). The method is useful for both *R. padi* and *M. granarium*. Although it is somewhat tedious, the aphid-injection method makes possible many studies that cannot be carried out by other methods.

The glass needles used for injections in our laboratory by W. C. Mueller, E-Wa Pang, or Anna Greenmun are prepared from

FIGURE 1. *R. padi* on a membrane after removal of membrane-covered tube from feeding cage. ×8.

two mm. tubing. Each needle is drawn three times over successively smaller flames and a final point is produced by chipping with a razor blade. The completed needles, which have a point diameter of 25-40μ, are fastened to rubber tubing connected to a rubber syringe bulb. To fill a needle, the operator places its tip in the test solution, presses the syringe bulb with his foot, and

allows solution to rise in the needle. Injection is usually made in the back of the aphid between the abdomen and thorax (FIGURE 2). Liquid is forced into the aphid by pressing with the foot on the syringe bulb. Use of the foot control allows both hands to be used for manipulation of the needle and holding the aphid by means of

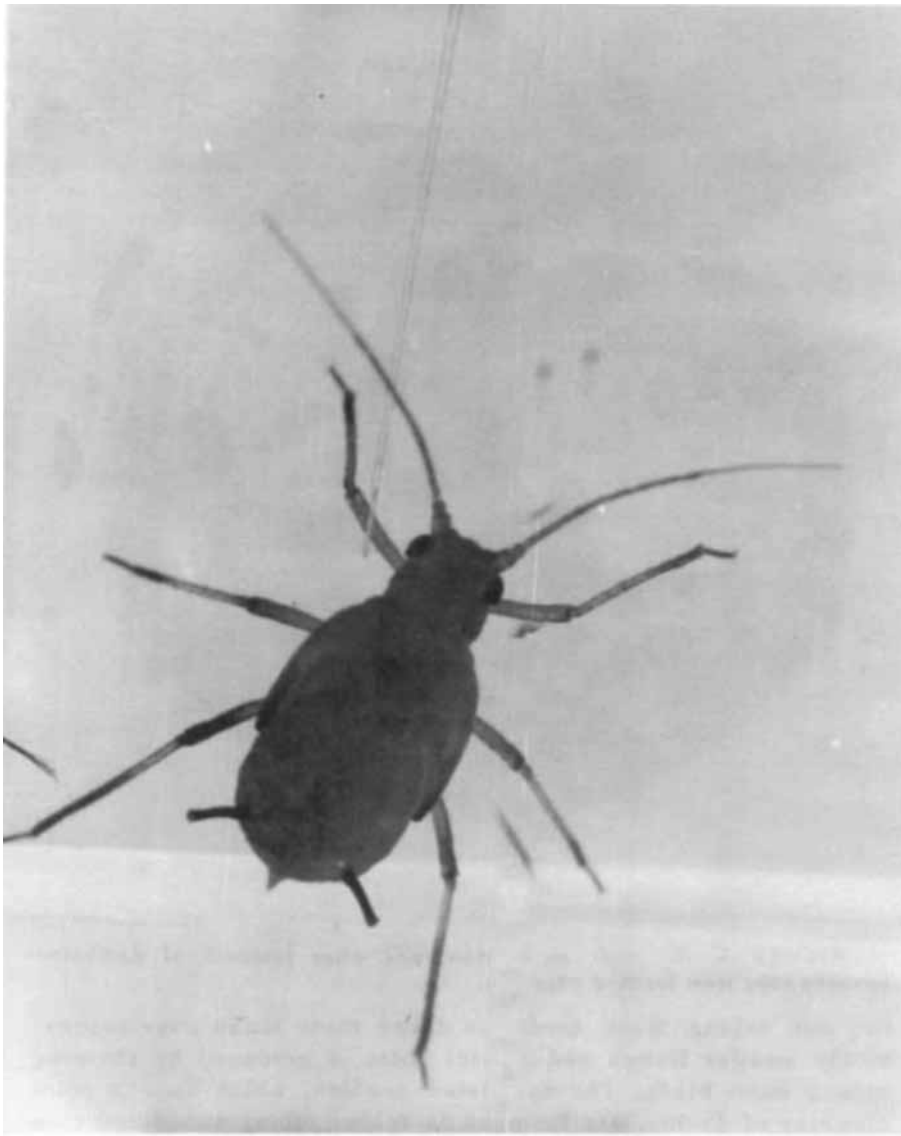

FIGURE 2. Glass needle being placed into position for injection of *M. granarium*. × 27.

a brush on the stage of a binocular microscope. Aphids are sometimes anesthetized by exposure to CO_2. Although injected aphids often transmit the virus within one day, an inoculation test-feeding period of five days is usually allowed.

Evidence for the Specificity. Isolates of barley yellow dwarf virus are maintained by us in oats (variety "Coast Black" or "California Red"). Virus cultures are transferred to new plants approximately every six weeks. Each transfer is carried out by cutting detached leaves into two or more pieces to allow a direct comparison of different aphid species. In early studies only *R. padi* and *M. granarium* were used. Currently 2 additional species (*R. maidis* and *T. graminum*) are used (Rochow, 1959*b*, 1959*c*). Following an acquisition feeding period usually of 48 hours at 15°C., about 10 aphids are caged on each of three oat seedlings for an inoculation test-feeding period of three to five days. An indication of the specificity of the two virus strains is given by results of one continuing transmission series that began in 1957 and has been carried to date through 32 serial transmissions. One strain (MGV) was transmitted to 144 of 146 plants by *M. granarium* but to none of 97 plants by *R. padi*. In contrast, in parallel tests with another strain (RPV), *R. padi* transmitted virus to 132 of 137 plants but *M. granarium* transmitted this virus strain only to 1 of 95 plants. These data suggest an absolute specificity for transmission of MGV by *M. granarium* and a nearly absolute specificity for transmission of RPV by *R. padi*.

Specificity also occurs when aphids are allowed to feed through membranes on liquid preparations of the two virus strains. At least some transmission by *M. granarium* occurred in every test on liquid preparations made from MGV-infected plants during a period of four years. No transmissions have been obtained by feeding *M. granarium* on preparations of RPV. Some transmissions of RPV, but not MGV, have been obtained by using *R. padi* in membrane feeding experiments.

The same specificity exists when the aphids acquire virus by injection instead of by feeding. In one series of injection tests, both *R. padi* and *M. granarium* transmitted only when inoculum of the vector-specific strain regularly transmitted by each species from leaves was injected. This relationship existed whether inocula had been prepared from infected plants or from viruliferous aphids (Mueller and Rochow, 1961).

Basis for the Specificity. When specific transmission by *M. granarium* was found to be very common in tests on New York field samples (Rochow, 1958*a*), the first explanation investigated was based on possible variation within *R. padi*. It seemed possible

that our colony of *R. padi* simply represented a clone that was a poor transmitter of barley yellow dwarf virus. Since the colony continued to transmit some isolates of the virus very efficiently, there was no indication of such variation. Moreover, when the regularly-used colony was compared with two other colonies of *R. padi*, results were the same for all three colonies (Rochow, 1958*a*).

Further tests on possible importance of variation within the aphid species were made in cooperation with G. W. Bruehl in Washington. When aphid colonies derived from those used by Bruehl were tested in our laboratory, both *R. padi* and *M. granarium* functioned as did our colonies of the same species in the transmission of vector-specific isolates (Rochow, 1958*b*). In addition, our colonies of *R. padi* and *M. granarium* transmitted as well as did the Washington ones in tests made by Bruehl (1958).

Tests on samples collected in different parts of the United States provide additional evidence that the specificity is not based on peculiarities of our aphid colonies. We found that transmission by *R. padi* or *M. granarium* depends largely on the source of samples. When samples from New York were tested, virus was transmitted from over 80 per cent of the samples only by *M. granarium* in tests made during the five past growing seasons (Rochow, 1960*b*). On the other hand, in parallel tests in one season made on samples from certain other areas, such as California and Illinois, barley yellow dwarf virus was recovered consistently by *R. padi (Rochow, 1959c).*

Taken together, the results of direct comparisons of different clones of *R. padi*, the results of comparisons of New York and Washington colonies of *R. padi* and *M. granarium*, and the importance of the virus-isolate in determining relative transmission by *R. padi* and *M. granarium* show that the major basis for the variation is in the virus rather than the aphids.

Mechanism of the Specificity. In some tests on specific transmission of barley yellow dwarf virus by *R. padi* and *M. granarium*, specificity has been absolute (Toko and Bruehl, 1959; Watson and Mulligan, 1960). In our tests, however, specificity has been relative, not absolute. We have observed occasional transmissions by means of the "nonvector" species, particularly if acquisition feedings longer than 48 hours had been used (Rochow, 1959*b*, 1961*b*). The occasional transmissions by "nonvectors" could have importance in understanding the basis for the specificity. They could represent selection by the "nonvector" of a mutant or of a different virus strain from a mixture. On the other hand, the occasional transmissions could represent actual transmission of the

virus strain in question and merely reflect the inefficiency of transmission of that particular virus strain by the "nonvector."

Tests on plants that became infected in occasional transmissions by a "nonvector" have supported the idea of inefficient transmission. When the ability of *M. granarium* and *R. padi* to transmit virus from leaves of such plants is tested by means of the detached-half-leaf method, the transmission pattern is that of the original strain, not that of a selection from it (Rochow, 1959*b*, 1961*b*). In other words, when plants that became infected by means of *M. granarium* in tests on RPV were tested, for example, the virus was subsequently transmitted only by *R. padi* and not by *M. granarium*. Watson and Mulligan (1960) also noted that the ability of a given aphid species to transmit barley yellow dwarf virus was not affected by previous transmissions by other less efficient vectors.

The mechanism controlling this specificity might be centered in any one, or in a combination, of three main areas: acquisition of virus from the plant, physiology of virus in the aphid after acquistion, or inoculation of virus to plants by the aphid vector. Two lines of evidence suggest that failure to acquire virus from a source plant is not the major basis for the specificity.

First, as mentioned above, specificity obtains whether acquisition is by feeding or by injection (Mueller and Rochow, 1961). Second, the "nonvectors" acquired virus in direct tests of the question (Rochow and Pang, 1961). Both *R. padi* and *M. granarium* were fed on oats infected by the strain each does not normally transmit. Although none of the aphids tested was able to transmit barley yellow dwarf virus, some individuals were found to be viruliferous in each of six experiments based on transferring hemolymph from single aphids to the aphid species that regularly serves as a vector for the strain in question. Since the virus in "nonvectors" had reached the hemolymph, the gut wall does not seem to be a barrier in this system as it is in some leafhopper systems (Storey, 1933; Sinha, 1960). A treatment has not yet been found that will enable the "nonvector" to transmit regularly such virus acquired in long feedings.

Another aspect of variation between *R. padi* and *M. granarium* in the transmission of strains of barley yellow dwarf virus is a difference between the two aphid species when virus transmissions are made from plants doubly infected by both MGV and RPV strains (Rochow, 1959*a*). When a source leaf is infected by both virus strains, as indicated by regular transmission of virus by both aphid species after acquisition feeding on opposite half-leaves, vector specificity still prevails with *M. granarium* but not with *R. padi*.

Results of repeated tests in our laboratory show that *M. granarium* transmits only MGV from such doubly infected leaves. In contrast, the strain or strains transmitted from doubly infected leaves by *R. padi* are subsequently usually transmitted regularly by both *R. padi* and *M. granarium* in our tests. In similar tests by Toko and Bruehl (1959), however, specificity for both aphid species was unaltered by transmission from doubly infected plants. The explanation for this phenomenon is not known, but the system appears to offer another approach to studies on the mechanism of the variation.

Two Groups of Virus Strains. Results of the various studies on vector specificity of barley yellow dwarf virus are perhaps best explained by assuming that the virus is extremely variable and that existing strains differ in the efficiency with which each aphid species can transmit them. The variations in transmission between *R. padi* and *M. granarium* would then be based on the existence of two groups of virus strains.

The first group of strains are those transmitted efficiently by *R. padi*. Isolates of this group seem to vary greatly in the efficiency by which they are also transmitted by *M. granarium*. Some strains, such as those described by Toko and Bruehl (1957) and Watson and Mulligan (1960), are not transmitted by *M. granarium*. Other strains, such as those studied in our laboratory, are acquired fairly readily (Rochow and Pang, 1961) but transmitted only occasionally by *M. granarium*. Still other strains may be transmitted as efficiently by *M. granarium* as by *R. padi*. All isolates of this group studied by us are also transmitted by *T. graminum*.

The second group includes strains transmitted efficiently by *M. granarium*. Vector specificity of this group is much more pronounced than that of the first group. These strains are transmitted very rarely, if at all, by *R. padi*, despite their occasional acquisition by this aphid species. Watson and Mulligan (1960) found such strains to be transmitted also by *Sitobion fragariae* (Walker) and *Metopolophium dirhodum* (Walker).

Future studies on these and other strains of barley yellow dwarf virus will undoubtedly contribute not only to an understanding of the variation in the aphid-virus relationship, but also to even more fundamental knowledge about the mechanism of aphid transmission of plant viruses.

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