J. gen. Virol. (1971), 10, 99–101
Printed in Great Britain

New Evidence on the Mechanism of Aphid Transmission of Potato C and Potato Aucuba Mosaic Viruses

(*Accepted 7 October* 1970)

A few plant viruses are unusual in that they are not transmitted by insects from plants in which they are present alone but are transmitted from plants also infected with another (helper) virus that is insect-transmitted. In all the reported instances, the helper virus has a species of aphid as its vector. They all fall into one of two groups, according to the manner of transmission by aphids of the helper virus. The helper virus may be *non-persistent*, when the aphids acquire and transmit the virus within a few min. but lose their ability to infect after a few probes on a healthy leaf, or it may be *persistent* (circulative), when the aphids need to feed on infected plants for long periods before becoming infective but then remain infective for a long period, during which they can infect several plants.

Viruses that have been transmitted by aphids in association with a non-persistent helper virus are potato aucuba mosaic virus (PAMV) aided by potato virus Y (PVY) or potato virus A (PVA) (Kassanis, 1961), and potato virus C (PVC) aided by PVY (Watson, 1960). Several viruses have been reported to be transmitted by aphids only in association with a persistent helper virus; tobacco mottle virus aided by tobacco vein-distorting virus (Smith, 1946); parsnip yellow fleck virus aided by anthriscus yellows virus (Murant & Goold, 1968); carrot mottle virus aided by red-leaf virus (Watson, Serjeant & Lennon, 1964); groundnut rosette virus aided by groundnut rosette assistor virus (Hull & Adams, 1968); barley yellow dwarf virus MAV isolate aided by RPV isolate (Rochow, 1970). The last pair differs from the others in that each isolate can be transmitted from plants infected by it alone and only by its specific aphid vector, whereas from plants infected by both, the MAV isolate can be transmitted by the vector of the RPV isolate.

Many suggestions have been made to explain how one virus may help the transmission of another, but only with barley yellow dwarf virus has good experimental evidence been provided to support any suggested mechanism. Rochow (1970) showed that, in plants infected with the two serologically unrelated isolates of barley yellow dwarf virus, the nucleic acid of the MAV isolate becomes coated with the protein of the RPV isolate, implying that the vector specificity of these two virus isolates depends on the virus protein. Sharing of the coat protein may explain the transmission of the other viruses aided in transmission by viruses that persist in aphids, but we have evidence that the transmission of the two viruses having non-persistent helper viruses (PAMV and PVC) has a different explanation.

We report here the results of experiments done with the non-persistent helper virus combinations to ascertain whether the virus needs to multiply or be present in the same plant as its helper. We tried consecutive acquisition feedings in which the aphids (*Myzus persicae* Sulz.) were allowed to probe for 1 to 2 min. first into a leaf infected with one virus and then into a leaf infected with the other virus of each pair before they were transferred to test plants. Groups of 15 to 20 aphids (*Myzus persicae* Sulz.) were starved for about 3 hr before feeding for 1 to 2 min. either on plants infected with both viruses or first on plants infected with one of the viruses and then on plants infected with the other. Each group of aphids was then transferred to a test plant, which was fumigated a few hr later. The acquisition feeds were on tobacco (*Nicotiana tabacum* L. cv. Xanthi-nc). The test plants for PAMV were pepper seedlings (*Capsicum annuum* L. cv. Long Red) on which this virus causes a characteristic systemic necrosis, and for PVC were tobacco seedlings. To distinguish PVC from PVY, the infected tobacco seedlings were tested by inoculating their sap mechanically to potato (*Solanum tuberosum* L. cv. Majestic). About a week after inoculation, PVC produced characteristic black necrotic local lesions, easily distinguished from the lesions produced later by PVY. When the aphids were fed first on plants infected only with the helper virus, PAMV and PVC were transmitted as efficiently as they were from plants infected with both, but they were not transmitted when the order was reversed (Table 1). Consecutive feeding has been tried with at least one virus having a persistent helper virus but without success (Smith, 1946).

Table 1. *Transmission of potato aucuba mosaic virus (PAMV) and potato virus C (PVC) with the help of potato virus Y (PVY)*

Treatment	Number of plants infected / Number of plants tested
PAMV+PVY (mixed infection)	15/25
PVY followed by PAMV	13/25
Healthy leaves followed by PAMV	0/14
PAMV followed by PVY	0/13
PVC+PVY (mixed infection)	6/6
PVY followed by PVC	6/6
PVC followed by PVY	0/6

Our results show that the help must be provided either at the aphid during acquisition of the aided virus or during injection of the virus into the test plant. The second possibility seems to be eliminated by: (1) aphids fed on leaves infected with PAMV alone failed to transmit it to plants already infected with PVY; (2) aphids fed first on plants infected with PVY and then on plants infected with PAMV transmitted PAMV to *Datura stramonium* L., which is immune to PVY.

Of the several suggestions put forward to explain the specificities reported in the transmission of non-persistent viruses, the most relevant to our results is the concept of 'mechanical surface adherence' (Pirone, 1969). Differences in surface structure of the stylets might account for differential absorption and elution, i.e. PAMV and PVC by themselves are not adsorbed to the stylets but PVY is, and when it is, it modifies the surface structure or charge of the stylets, thus allowing PAMV or PVC to be adsorbed either on to the modified stylet surface or on to the PVY particles.

PAMV and PVY are serologically unrelated and seem not to compete when present in the same plant (Kassanis, 1961), so an aphid might acquire both viruses during a single probe. This is less probable with PVC and PVY, which are very closely related, compete with one another and are therefore probably irregularly distributed in the leaf. Therefore, transmission of PVC from plants infected with both viruses probably happens after two consecutive probes, the first in a region containing PVY and the second in a region containing PVC. Watson (1960) suggested that the transmission of PVC from plants also infected with PVY depends on genetic recombination between the two, but our results show that there is no need to postulate this to explain the transmission.

Other of our results (not produced here) show that the feeding periods on the successive source plants are no more critical than for transmission of the aiding virus alone and therefore, in natural surroundings, transmission by consecutive feeding could be frequent because winged aphids often move from plant to plant.

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(*Received* 25 *September* 1970)