Interactions of insect vectors with plants in relation to transmission of plant viruses

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Abstract. Information on the mechanism of viral acquisition by insect vectors and the interactions therein appears to be inadequate, and the differential responses of the vectors to different plant species appear to influence the virus transmissibility. High transmissibility is found in plants which have high susceptibility to both viruses and vectors. The vectors having low preferences for particular plant species show their inefficiency in transmitting viruses in those plants. Differential acquisition of virus is found even in different varieties of the same species. Different vectors of a particular virus may show differential capability of transmission in different hosts. The host specificity of the vectors also partially explains the virus specificity in plants. But in-depth information on the differential transmissibility due to vector-host interactions is not yet available. Further the loss of transmissibility by vectors due to feeding on some unfavourable hosts and due to mixed feeding of vectors and non-vector species of insects on some hosts, etc., have also not yet been adequately studied. Detailed study on the effect of insect vector-host interactions on the plant virus transmission may unravel a new biological method for the control of the plant virus disease in future.

Keywords. Insect vectors; plant virus; differential transmissibility.

1. Introduction

Certain groups of insects, particularly aphids, plant and leafhoppers, beetles and whiteflies transmit most of the plant viruses. This specificity of vectors with respect to viruses may also be related with the vector-host interactions. The viruses are known to have three types of relationships with their vectors, namely nonpersistent (styletborne), semi-persistent (circulative) and persistent (propagative). Although these relationships are primarily classified on the basis of the period of retention of the viruses in their vectors, the acquisition of these viruses from the hosts may involve different host-dependent processes. The efficiency of transmission of different viruses by different vectors to different hosts may also be a host-dependent process. These phenomena suggest that insect transmission of viruses may depend upon the interactions between the insect vectors and the hosts. The details of such interactions need to be known and the implications of such interactions for the cultural control of pests also need to be explored.

2. Insect vectors of plant viruses

There are about 400 species of phytophagus insects which can transmit plant viruses. These vector species primarily belong to Aphididae (aphids), Auchenorrhyncha (leaf and planthoppers) and Coleoptera (beetles). There are about 200 aphids, 60 leaf and planthoppers and 30 beetles which transmit more than 215 different viruses. The other insect vectors are Coccidae (mealy bugs), Aleyrodidae (whiteflies) and Thysanoptera

(thrips) which altogether transmit 30 different viruses of which 25 viruses are transmitted by only 6 species of whiteflies (table 1).

The aphids apparently represent a versatile group of vectors. There are about 27 genera of aphids which act as vectors. The largest number of viruses however are transmitted by the genus *Myzus*. Amongst the species of *Myzus* again, *Myzus persicae* is the most common vector. It transmits more than 60 different viruses.

The aphids again show a wide variability in virus transmissibility. Onion yellow dwarf and cucumber mosaic virus are transmitted by 50 aphid species each. The cauliflower mosaic virus is transmitted by about 25 aphid species. There is again a large number of viruses which are transmitted by only one aphid species each.

The leaf and planthoppers are very specific with respect to virus transmissibility. Majority of the viruses are transmitted by only one leafhopper species. There are, however, several viruses, which have more than two leafhopper vectors such as maize streak, potato yellow dwarf, rice tungro and wound tumor. There is no species of leafhopper which has wide versatality in transmitting a large number of viruses as shown by *M. persicae*. In case of whiteflies, most of the viruses reported so far, are transmitted by *Bemisia tabaci*. In beetles, on the other hand, there is no single species which has specialized as a versatile vector like *M. persicae* or *B. tabaci*. Barring a few, most of the viruses are transmitted by specific-beetle species.

3. Feeding behaviour and virus transmission

The feeding behaviour of aphids, leaf and planthoppers and whiteflies differs from that of beetles. All aphids, leafhoppers and whiteflies possess piercing and sucking mouth parts; the beetles on the other hand have biting mouth parts. The mouth parts of aphids and leafhoppers consist mainly of two pairs of stylets held together by longitudinal

Table 1. Range of known insect vectors of plant viruses and virus-like agents.

Taxonomic group	Approximate number of vector species	Approximate number of viruses transmitted
Hemiptera		
Aphididae (aphids)	200	160
Psyllidae (psyllids)	1	1
Coccidae (mealy bugs)	15	2
Aleyro didae (whiteflies)	3	25
Auchenorrhyncha (leaf and planthoppers)	60	35
Gymnocerata (tingid bugs)	2	2
Coleoptera (beetles)	30	20
Thysanoptera (thrips)	6	3
*Orthoptera**	10	6
*Dermaptera**	1	1
*Lepidoptera** (moths)	4	5
*Diptera** (flies)	2	3

* Vectors in these taxa are considered to be of little biological importance. (after Gibbs and Harrison 1976).

ridges and grooves on their adjacent surface, a labium, a large slender rigid organ with a deeply concave anterior surface forming two channels of beak, a labrum, mandibles and maxillae. The two pairs of stylets form a compact bundle or fasicle which slides in the groove of labium and constitutes the piercing organ. The piercing organ has two canals, through one (salivary canal) saliva is injected into a plant and through the second (food canal) food is sucked up from the plant. The beetle vector species usually lack functional salivary glands (Markham and Smith 1949). It has been suggested that the virus transmission by the beetles is associated with the process of regurgitation (Walters 1969). Thus the interactions between the sucking type of vectors and the biting type of vectors are different, particularly with respect to virus transmission. The saliva-plant interaction is important in case of the sucking type of vectors, whereas the interaction between the plant constituents and the regurgitating fluid is important in case of the biting type of vectors.

Extensive research has been conducted on the feeding behaviour of the sucking type of vectors (Nault and Gyrisco 1966). It has been demonstrated that aphids and leafhoppers usually secrete two types of saliva, sheath materials which coagulates rapidly and forms a salivary sheath or stylet sheath in the path of stylets and water soluble saliva (Miles 1968). Most of the aphids and leafhopper form this sheath around their stylets during the feeding process. Stylet sheath is laid by the vector in the tissue of the host and it stays there even on withdrawal of stylets. It shows the intercellular (in case of aphids) and interacellular (in case of leafhoppers) path that the stylets follow during passage through tissues and also the point where it terminates. Stylets move fairly rapidly within this sheath but it subsequently extends beyond the sheath for ingestion of food materials from the host cells. In the head of the vectors, there are food and salivary pumps, which help to regulate the flow of food material and saliva. The process of regurgitation is also apparent in the feeding process (Garrett 1973).

The feeding process of vectors involves interactions between the vectors and hosts. These interactions are also involved in virus transmission. The scale of feeding on different host in the virus transmission has been demonstrated in several host-vector-virus combination. Hinz (1969) found higher transmission of sugar-beet mosaic and beet yellow by proper feeding of the vector on *Physalis floridiana*. Similar observations have also been made with potato leaf roll virus. Thus it is apparent that the vector-host interactions may participate in virus transmission. Such participations may be in the availability of primary nutrients and characteristics of the minor constituents of plant sap, identification of feeding sites by the vectors, interaction of the cell sap in the formation of salivary sheath and the regurgitation of the cell sap in the vectors.

4. Host-vector-virus specificity

The insect vectors always have a set of host range. The study on the feeding tracts of an insect in different plant species revealed the differences in the extent of feeding on them (Day *et al* 1952; Carter 1973). These differences in feeding are often utilized to explain not only the host specificity of the vectors but also the virus specificity of the hosts. A host more susceptible to a vector is usually more susceptible to the virus. When the relative susceptibility of Pankhari-203, Latisail, T(N)1 and others to RTV and *N. virescens* was tested, such relationship was found (tables 2 and 3). Critical analysis may however tend to indicate that host specificity for vectors and viruses may not be due

Table 2. Tungro transmission and seedling infection by viruliferous *Nephotettix virescens* on 10 rice varieties.

Variety	Insects		Reten-sion (days)	Seedlings		Infected	
	Tested (No.)	Infec-tive (%)		Inocu-lated (No.)	Infec-tion (%)	No./ insects	No./ Infective insects
Ambemohar	40	45	1·27	182	12·6	0·57	1·27
Gampai 30-12-15-	40	35	1·07	168	8·9	0·37	1·07
Habiganj DW-8	40	7·5	1·00	160	1·8	0·07	1·00
IR-26	40	67·5	1·40	183	20·7	0·95	1·40
IR-34	40	37·5	1·13	159	10·7	0·42	1·13
Kataribhog	40	15	1·16	187	3·7	0·17	1·16
Latisail	40	75	1·76	192	27·6	1·32	1·76
Pankhari 203	40	17·5	1·14	173	4·6	0·20	1·14·
Ptb 18	40	40	1·18	169	11·2	0·47	1·18
TN1	40	82·5	1·54	193	26·4	1·27	1·54
Total/Av.	400	42·2	1·26	1766	12·8	0·58	1·26

Table 3. Differential transmission of different strains of rice tungro virus by *Nephotettix virescens* and *Nephotettix nigropictus* in T(N)1 seedlings.

Virus	Percentage of transmission	
	N. virescens	*N. nigropictus*
RTV$_{2B}$	72	Nil
RTV$_3$	80	20
RTV$_4$	52	32

to identical reasons in all cases. The feeding ecology of herbivorous insects depends upon the availability of primary nutrients and on the level of toxic or infering minor constituents of the cell sap (Mitchel 1981). The virus susceptibility of the hosts may depend only upon the level of toxic or interfering constituents of the cell sap. T(N)1, IR-8 and Vijoya which show differential susceptibility to *Nephotettix virescens*, possess quantitatively different levels in some primary nutrients (table 4). The effect of nutrients on feeding was more convincingly showed by Wenster (1962) who found that sinigrin (a mustard oil glucoside from Brassicas), when introduced into bean leaves induces the aphid *Brevicoryne brassicae* to feed and produce young ones on this host when normally it would not. The effect of these nutrients on the susceptibility to viruses has not yet been studied. The nutrients or minor constituents of a host that affect the feeding behaviour of a vector, may also effect the virus susceptibility in certain host-vector-virus combinations. In many other cases however, the differential feeding behaviour alone cannot explain the differential transmission of viruses. Differences in the extent of transmission of a particular virus occur with different vector species having similar feeding efficiency in a particular host. The feeding efficiency of *Nephotettix virescens* and *Nephotettix nigropictus* on T(N)1 does not differ. *Nephotettix virescens* transmits all the strains of rice tungro virus (RTV) in T(N)1. *N.*

nigropictus can transmit only RTV_4 in the same plant species. The extent of transmission of RTV_4 by *N. virescens* and *N. nigropictus* differs (table 3). These differences in transmission may be due to differential reaction of the host with the vector. Mukhopadhyay and Chaudhuri (1973) demonstrated the differential transmission of RTV from different source plant (table 5). When a particular vector species transmits different strains of a particular virus, the efficiency of transmission may also differ. *N. virescens* transmits RTV_1, RTV_{2B}, RTV_3 and RTV_4. The percentages of transmission of these strains by *N. virescens* to T(N)1 plants differ (table 3). The differential transmission of different strains of viruses by a particular vector may not be related to feeding behaviour, but it may depend upon the host-vector-virus interactions involved in the mechanism of the acquisition and inoculation processes of viruses in the hosts.

5. Mechanism of transmission under different virus-vector-host interactions

The nonpersistent viruses are usually localized in nonvascular tissues. These viruses are acquired and inoculated in these tissues. Circulative viruses are accessible in phloem tissues although inoculation may occur in nonvascular tissues. Acquisition is expected to begin with injestion of phloem sap. The persistent or propagative viruses are acquired from vascular tissues and inoculated also to the same tissues.

Table 4. Quantitative differences in nutrients in the leaves of different varieties of rice having differential susceptibility to *Nephotettix virescens*.

Nutrients	Contents in different varieties of rice		
	T(N)1	IR-8	Vijoya
Total sugar (mg/g)	50·0	48·0	53·0
Reduced sugar (mg/g)	5·5	5·5	5·4
Nonreduced sugar (mg/g)	44·5	42·5	47·5
Phosphorus (ppm)	4177·0	3520·8	3729·2
Nitrogen (%)	1·9	2·7	2·5
Iron	366·7	391·6	333·3
Manganese	302·1	250·0	458·3

Table 5. Ability of *Nephotettix virescens* to transmit RTV from different source plants.

	Percentage of transmission in T(N)1 seedlings		
	Crop seasons		
Source variety	Aus (Autum rice)	Aman (Winter rice)	Boro (Summer rice)
IR-8	60	55	85
Jaya	60	65	75
Padma	80	90	90
Latisail	15	25	30

IRC News letter, (1973)

Nonpersistent viruses are usually acquired during superficial probes. They are more readily acquired during brief probes than the longer ones. The transmission threshold period can be as short as 2 min, also the viruses can be efficiently acquired and inoculated during probes of only 10 to 30 sec. The host-vector-virus interactions in all these three categories of vector-virus relations are little understood. In nonpersistent viruses, host factor is primarily involved in the mechanism of transmission, as the respective viruses are not retained in the vectors; in semipersistent and persistent viruses on the other hand, the viruses are retained in the respective vectors for different periods and thus their transmissibility is also dependent on the extent of interactions within the vector tissues. In circulative viruses, virus accumulates in the gut as feeding on a source plant continues. Some of the ingested virus is actively moved through the gut wall into the hemocoele, and some are excreted. Once in the hemocoele, the virus can be transported in the hemolymph and may accumulate in specific tissues. Eventually the virus is actively moved through the salivary system. The virus is introduced into plants with salivary material during stylet penetration and the establishment of a feeding site. Inoculation can occur in both vascular and non-vascular tissues. Virus release is a periodic rather than a continuous event during feeding, since release is associated with salivation and presumably not with ingestion. Semipersistent viruses do not multiply in the vectors whereas the persistent viruses multiply in the specific tissues of the vector. Many experimental results suggest that nonpersistent viruses are carried on, in or near the mouthparts. The actual mechanism for the transmission of this type of viruses has not yet been adequately explained. Some workers suggested it as a physical attachment of virus particles on the mandibular stylets which have a series of ridges, others suggested the holding of the particles in food canal and still others believed the involvement of the gelled saliva. The production of the plug of gelled saliva at the site where the stylets puncture the leaf (Sylvester 1962) is a function of the interaction between the saliva and sap constituents. Information in this regard is however very limited. Research on such interactions may unravel the truth in future. Garrett (1973) found the correlation between the regurgitation of sap and the aphid transmission of viruses. The regurgitation process reflects interaction between the plant sap and the vectors. How such interaction leads to virus transmission is not yet known. Govier and Kassanis (1974) identified the existence of a transmission factor in the plant sap. This factor is also to be acquired by the vector for virus transmission. Potato aucuba mosaic virus and potato virus C which are not usually transmissible by aphids, could be easily transmitted by *Myzus persicae* when these viruses are acquired by the vector along with the transmission factor. The mechanism of transmission of nonpersistent viruses involves two processes namely acquisition and inoculation. An additional process of retention is involved in the transmission of semi-persistent and persistent viruses. Both acquisition and inoculation are host-dependent processes. The modes of participation of the host tissues in the transmission may differ with different combinations. There may be interfering or promoting substances or there may be additional transmission factor.

6.   Vector host interactions in disease complexes

Host-vector-virus interactions become more complicated in diseases complexes in which the vector transmissibility of a virus depends upon the participation of another

dependent virus or assistor virus component. Smith (1946) found that aphids could transmit tobacco mottle virus only from the plants that are also infected with vein distorting virus. The mottle virus alone is juice inoculable but not aphid transmissible. Hull and Adams (1968) found similar dependence of groundnut assistor virus. The presence of assistor viruses has also been reported in several other disease complexes such as dependent carrot mottle and assistor, carrot red leaf (Watson *et al* 1964), lettuce and beet western yellow virus (Falk 1978), tobacco yellow vein and tobacco yellow vein assistor virus (Adams and Hull 1972) etc.

Another interesting disease complex has been found with respect to physalis yellow net disease (Weidemann 1971) and turnip latent virus disease (Mackinnon 1956). Although both the diseases result from simultaneous infection with two viruses, neither of them are juice inoculable or truly dependent upon the other for aphid transmission (Mackinnon 1965). Mackinnon and Lawson (1966) found that physalis mild chlorosis virus could be easily isolated from the mixture which is efficiently transmitted by aphids. The physalis vein blotch component, which is aphid transmissible in mixture, could hardly be transmitted by aphids when isolated in pure form.

The phenomenon of the complex diseases suggests complicated vector-host-virus interactions. Presence of dependent or assistor viruses may change the intra- or intercellular environment which may influence the vector-host interactions leading to virus transmission. These microlevel cellular environment and interactions, however, are yet to be studied.

7. Vector host interaction in host passage effects

Continuous passage of different viruses through the hosts or vectors may alter the transmissibility of the concerned viruses by their vectors. Passage of virus through plants may affect the ability of insect vectors to acquire the virus and the passage of the virus through insects may affect the ability of the insect vector to transmit the virus to plants. Black (1953) found that potato yellow dwarf virus could no longer be transmitted by its vectors after 16 yr of mechanical transmission. Black *et al* (1958) found that wound tumor virus lost its ability to be transmitted by its vector after several years of vegetative propagation in *Melilotus officinalis*. Liu *et al* (1973) found that this loss occurred in several progressive steps and was accompanied by a decline of concentration of virus in the texmors. Reddy and Black (1974, 1977) found that the loss of vector transmission was also associated with a loss of segments of the mechanical transmission to soybean or *Arachis hypogea*. Koika (1978) found that the ability of the aphid *Dactynotus ambrosiae* to transmit a strain of sugarcane mosaic was lost after the virus was vegetatively transmitted in and mechanically transmitted to sorghum bicolor for 15 yr.

8. Discussion

Insect vector relations to the hosts are intimately connected with the transmission of plant viruses. All the phytophagous insects are not vectors. There occurs specificity of the vectors with respect to viruses. The specificity may be of varied types and may depend upon host-vector interactions. A large number of vectors may transmit a

particular virus, but the efficiency may differ. The difference in transmission efficiency of this type may primarily depend upon the differences in feeding behaviour and relative susceptibility of the vectors to the hosts. The hosts which are more susceptible to vectors may show higher transmission. The susceptibility of the hosts to different vectors may depend upon the availability of primary nutrients and minor chemical constituents of the plant sap which may promote or interfere with the feeding behaviour. In differential transmission of different strains of a particular virus by a particular vector to a particular host, the host-virus-vector interactions involved in the mechanism of the transmission may play an important role. The mechanism of transmission may be different under different virus-vector relations. In nonpersistent viruses, acquisition and inoculation processes determine the extent of transmission. An additional process of retention and circulation of the virus in the body of the vector takes place in the transmission of semi-persistent and persistent viruses. The acquisition and inoculation of viruses by vectors are host-dependent processes. The extent of these processes may depend upon the presence of promoting or interfering or inhibiting substances, presence of transmission factors or assistors in the cell sap or the interactions between the virus, cell sap, vector saliva and other vector constituents during regurgitation of the food ingested by the vector insects. The virus-vector-host interactions, become more complicated in case of complex diseases. In such diseases, the transmission of one virus depends upon the presence of another virus. In extreme cases a virus appears vector transmissible only under the mixed infection condition. Under these circumstances, the concerned viruses may have genetic complements or there may be change in the cellular microenvironment to induce changes in the vector relations. Another form of complexity is apparent in the continuous host passage of viruses. In several such cases either new strains may develop which may show vector transmissibility in contrast to the nonvector transmissible parental forms. There are also cases, where continuous host passages have resulted loss of vector transmissibility.

The insect vector-host relations are apparent in nature particularly with respect to the transmission and evolution of plant viruses. Such relations have both agricultural and ecological values. From the agricultural view point, an understanding of such relations may be utilized to reduce the transmission of viruses either by developing suitable agroecosystem or by genetic manipulations to induce reduction in transmissibility. The agricultural utilizability of such relations is still a hypothesis and needs intensive research. The ecological values of insect vector-host relations are apparent from the records available in this regard, several new strains have evolved in nature, and several viruses attenuate due to the loss of their transmissibility. The evolution of new strains and attenuation of existing viruses, are to affect the ecology of viruses, which may ultimately affect the ecosphere. The evolutionary significance of this insect-vector-host interactions needs extensive systemic study.

References

Adams A N and Hull R 1972 Tobacco yellow vein a virus dependent on assistor virus for its transmission by aphids; *Ann. Appl. Biol.* **71** 135–140

Bird J and Maramorozh K 1978 Viruses and virus diseases associated with whitefly; *Adv. virus Res.* **22** 55–106

Black L M 1953 Loss of vector transmissibility by viruses normally insect transmitted; *Phytopathol.* **43** 466

Black L M, Wolcyrz S and Whitecomb R F 1958 *7th Int. Cong. Microbial.* Abstr. No. A14

Carter W 1973 *Insect in relation to plant diseases* (New York: John Wiley)

Day M F and Irzykiewicz H 1954 On the mechanism of transmission of non-persistent phytopathogenic viruses by aphid; *Aust. J. Biol. Sci.* **7** 251–273

Falk B W 1978 *The etiology and transmission properties of the viruses inciting the speakles disease of letture,* Ph.D. thesis, Univ. California, Berkeley, 118 pp.

Garrette R G 1973 Non persistent aphid borne viruses in *Viruses and invertibrate* (ed) A J Gibbs *et al* (New York: American Elsevier) pp. 476–492

Gibbs and Harrison 1976 *Plant virology; The principles* Edward Aronlogy p. 185

Govier D A and Kassassis B 1974 Evidence that a component other than a virus particle is needed for aphid transmission of potato virus Y; *Virology* **57** 285–286

Hinz B 1969 Influence of food plants on vector capacity of aphids (Myzus perrical) *Zentralbl. Bakteriol. Infection-skrankh.* HY9. NW. Abt. **123** 230–236

Hull R and Adams A N 1968 Groundnut rosette and its assistor virus; *Ann. Appl. Biol.* **62** 139–145

Kimura H W and Black L M 1973 Specific infectivity of different wound tumor virus isolet; *Virology* **51** 320

Koika H 1978 *Phytopathol. News* 12–22

Mackinnon J P 1956 A virus latent to turnips; *Can. J. Bot.* **34** 131–134

Mackinnon J P and Lawson F L 1966 Transmission of vein blotch virus of *Physalis floridane* by aphids; *Can. J. Bot.* **44** 1219–1291

Markham R and Smith K M 1949 Studies on the virus of turnip yellow mosaic; *Parasitology* **39** 330–342

Mitchel R 1981 Insect behaviour resource exploitation are filness; *Annu. Rev. Int.* **26** 373–376

Mukhopadhyay S and Chowdhury A K 1973 Some epidemiological aspects of tungro virus disease of rice in West Bengal; *IRC Newslett.* **22** 44–57

Nault L R and Gyrisco G G 1966 Relation of the feeding process of the pea aphid to the inoculation of pea enation mosaic virus; *Ann. Entomol. Soc. Am.* **59** 1185–1197

Reddy D V R and Black L M 1966 Deletion mutation of the genome segments of wound tumor virus; *Virology* **61** 458–473

Reddy D V R and Black L M 1977 Isolation and replication of mutant population of wound tumor virions lacking certain genomic segments; *Virology* **80** 336–346

Smith K M 1946 The transmission of a plant virus complex by aphids; *Parasitology* **37** 25–37

Smith K M 1965 Plant virus vector relationships; *Adv. Virus Res.* **11** 61–65

Sylvester E S 1962 Mechanism of plant virus transmission by aphids, in *Biological transmission of disease agents* (New York: Academic Press)

Sylvester E S 1980 Circulative and propagative virus transmission by aphids; *Annu. Rev. Entomol.* **25** 257–286

Walters H J 1969 Beetle transmission of plant viruses *Adv. Virus Res.* **15** 335–363

Watson M A, Seojeant K and Lennon E A 1964 Carrol motley dwarf and parsnap mottle viruses; *Ann. Appl. Biol.* **54** 153–166

Weidemann H L 1971 Karyometrische Untersuchungen an der Hauptspeicheldriise Von *Myzus percical* 11. Kerngrossenanderungen nach Sauqen auf *Physalis floridane* Pflanzen die mitdem Blattro virus der Karto Hel (Potato leaf roll virus) in fiziert waren; *Entomol. Exp. Appl.* **14** 161–174

Wenster R J D 1962 Mode of host selection by an aphid; *Nature (London)* **195** 830–831