AUCHENORRHYNCHOUS VECTORS OF PLANT VIRUSES: VIRUS-VECTOR INTERACTIONS AND TRANSMISSION MECHANISMS

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ABSTRACT

Certain animals, or more specifically, arthropods and nematodes, are responsible for transmitting a number of plant pathogens, including viruses, mycoplasma-like organisms, spiroplasmas, rickettsia-like organisms, bacteria, and fungi. For transmission to occur, pathogen, vector, and host populations must overlap (spatially and temporally) and interact in a manner compatible with the requirements of pathogen acquisition, carryover, and inoculation. The study of pathogen-vector-host compatibility and how it is influenced (as measured by pathogen spread or vector transmission efficiency) by various biotic and abiotic components of the environment might be referred to as <u>transmission ecology</u> (Harris, 1978a, 1982). The scope of transmission ecology discussed here is mainly limited to times in the transmission cycle when pathogen, vector, and host come together. Special emphasis is placed on how pathogen-vector-host interactions are mirrored in observable transmission phenomena and how they define transmission mechanisms. The transmission systems are horizontal and comprised of viruses, auchenorrhynchous vectors, and plant hosts (Harris and Maramorosch, 1977, 1980, 1982; Maramorosch and Harris, 1979, 1981).

INTRODUCTION

There are about 383 known species of animal vectors of plant viruses (Harris, 1981a). About 94% of these vectors are arthropods, and the remainder are nematodes. Of the 358 known arthropod vectors, 356 are insects and 2 are mites. About 273 (76.4%) of the insect vectors belong to the order Homoptera: 214 species in the Sternorrhyncha and 59 in the Auchenorrhyncha. The transmission systems discussed here include viruses only and vectors in the Auchenorrhyncha: leafhoppers (Cicadellidae), treehoppers (Membracidae), and delphacid planthoppers (Delphacidae).

CATEGORIZING TRANSMISSIONS

Virus transmissions by homopterous vectors may be classified as <u>noncirculative</u> (including nonpersistent and semipersistent subcategories) and <u>circulative</u> (including nonpropagative and propagative subcategories) (Harris, 1981a). In circulative transmission, virus is acquired via the maxillary food canal, absorbed, translocated and--following a latent or incubation period in the vector--inoculated to plants in virus-laden saliva ejected from the maxillary saliva canal during probing and feeding: an <u>ingestion-salivation mechanism</u> of transmission. Circulative viruses may be further characterized as either nonpropagative or propagative, depending on demonstrability of virus nonmultiplication or multiplication, respectively, in the vector (Harris, 1981a).

The noncirculative (some believe stylet-borne) mode of transmission is characterized by the absence of a detectable latent period, loss of vector inoculativity through molting (nontransstadiality), and the lack of evidence for transmissible virus entering the hemocoele and exiting via the vector's salivary system. Assumedly, all transmissions that are referred to in the literature as nonpersistent or semipersistent meet at least the first two of these criteria, but relatively few reports have been made on the third criterion. Similarly, many persistent viruses have been classified as circulative solely on the basis of transstadial passage, the presence of a latent period, and analogy with known circulative viruses. Thus far, this assumed synonymity of terminologies (i.e., nonpersistent and semipersistent with noncirculative, and persistent with circulative) appears to be a prescient conclusion (Harris,1979). Numerous observable phenomena serve to separate noncirculative transmissions into the aforementioned nonpersistent and semipersistent subcategories (Harris, 1981a).

Nonpersistent, noncirculative transmission appears to be an epidermal and intracellular event. This kind of transmission, which is not known for auchenorrhynchous vectors, typifies many of the associations between plant viruses and sternorrhynchous vectors, specifically aphids. Sap-sampling or host-selection behavior plays an important, if not essential, role in the transmission process. Sap-sampling behavior is stimulated by subjecting aphids to preacquisition starvation. Sap-sampling on a virus-infected plant serves to contaminate the foregut with virus-laden material ("cell sap" or protoplasm). The transmission cycle is completed when all or an infective portion of this virus-laden material is egested during subsequent sap-sampling probes in healthy plants: an ingestion-egestion mechanism of transmission. This host-selection behavior serves to bring plant material in contact with the pharyngeal gustatory organ, permitting a quantitative and qualitative analysis of the plant's suitability as a host.

Semipersistent, noncirculative transmission is also compatible with an ingestion-egestion mechanism of transmission (Harris, 1977, 1978a, 1979). Semipersistence and increases in the probability of transmission, as well as in the duration of retention of inoculativity, with increases in the duration of the acquisition access feeding period (AAFP) suggest that virus can accumulate in the foregut and resist being quickly dissociated from the vector by egestion or flushing through with virus-free sap ingested from healthy plants. As is noted below, there are only two known instances of auchenorrhynchous vectors transmitting virus in a semipersistent, noncirculative manner. Both instances involve leafhoppers.

CICADELLIDAE

Leafhoppers, with 130 known vector species and subspecies covering 10 subfamilies and 58 genera, transmit about 71 disease agents (about 33 viruses, 31 mycoplasma-like organisms, 3 spiroplasmas, and 4 rickettsia-like organisms) and account for more than 80% of all auchenorrhynchous vectors (Nielson, 1978; Chiykowski, 1981; Harris, 1981). Twenty genera and 34 species of leafhoppers are responsible for the transmission of 33 viruses (Table 1). Most leafhopper-borne viruses are transmitted circulatively, and many of these are known to be propagative in their vectors. Leafhopper-virus interactions and circulative transmission characteristics have been reviewed recently in great detail (Harris, 1979) and, therefore, will not be repeated here.

Maize chlorotic dwarf virus (MCDV) and the viruses responsible for tungro and tungro-like diseases of rice such as waika, penyakit merah, penyakit habang, mentek, and yellow-orange leaf are exceptional in that leafhoppers transmit them semipersistently. These diseases resemble one another in symptomatology, mode of virus transmission, and cultivar reaction. Furthermore, they apparently are caused by similar isometric or bacilliform virus particles, or both, that share a common vector, *Nephotettix virescens* (Distant) (Hibino *et al*., 1978, 1979). Their transmission is further characterized by the absence of a detectable latent period and of evidence

Table 1

Auchenorrhynchous vectors of plant viruses

Vector taxa	Viruses
Cicadoidea	
Cicadellidae	
Aceratagallia curvata Oman	(New York) potato yellow dwarf (NY-PYDV)
A. longula (Van Duzee)	NY-PYDV
A. obscura Oman	NY-PYDV
A. sanguinolenta (Provancher)	NY-PYDV
Agallia constricta Van Duzee	(New Jersey) NJ-PYDV, wound tumor (WTV)
A. quadripunctata (Provancher)	NJ-PYDV, NY-PYDV, WTV
Agalliopsis novella (Say)	NJ-PYDV, NY-PYDV, WTV
Austroagallia torrida Evans	(Clover or Datura) rugose leaf curl[a]
Baldulus tripsaci Kramer & Whitcomb	Maize rayado fino (MRFV)
Cicadulina bipunctella bimaculata Evans	(Rice and maize) leaf gall[a], maize wallaby ear (MWEV)[a]
C. bipunctella zeae China	Maize streak (MSV)
C. latens Fennah	MSV
C. mbila (Naudé)	Eastern wheat striate, MSV
C. parazeae Ghauri	MSV
C. storeyi China	MSV
Circulifer tenellus (Baker)	(North American) sugar beet curly top
Dalbulus elimatus (Ball)	MRFV
D. maidis (De Long & Wolcott)	MRFV
Draeculacephala portola Ball	Sugarcane chlorotic streak
Endria inimica (Say)	(North American) wheat striate mosaic (NA-WSMV)
Elymana sulphurella (Zetterstedt)	NA-WSMV
Graminella nigrifrons (Forbes)	Maize chlorotic dwarf (MCDV), oat striate mosaic
G. sonora (Ball)	MCDV
Macrosteles fascifrons (Stål)	(North American) oat blue dwarf
M. laevis (Ribaut)	(Swedish) oat blue dwarf
Nephotettix cincticeps (Uhler)	Rice bunchy stunt[a], rice dwarf (RDV), rice gall dwarf (RGDV)[a], rice transitory yellowing (RTYV), rice waika (RWV)
N. malayanus Ishihara & Kawase	RGDV, RWV
N. nigropictus (Stål)	RDV, RGDV, RTYV, rice tungro (RTV), RWV, rice yellow-orange leaf (RYOLV)
N. virescens (Distant)	Penyakit merah, penyakit habang, RBSV, RGDV, rice leaf yellowing, rice mentek, RTYV, RTV, RWV, RYOLV
Nesoclutha pallida (Evans)	Cereal chlorotic mottle, Chloris striate, MWEV[a], Paspalum striate[a]
Orosius argentatus (Evans)	Bean summer death, tobacco yellow dwarf
Psammotettix alienus (Dahlbom)	(Russian) winter wheat mosaic (R-WWMV)
P. striatus (Linné)	R-WWMV
Recilia dorsalis (Motschulsky)	RDV

Table 1 (Continued)

Vector Taxa	Viruses
Cicadoidea (continued)	
Cicadellidae (cont'd)	
Scaphytopius albifrons Hepner	(Texas) cotton yellow vein
Stirellus bicolor (Van Duzee)	MRFV
Membracidae	
Micrutalis malleifera Fowler	(Tomato) pseudo-curly-top disease
Fulgoroidea	
Delphacidae	
Delphacodes propinqua (Fieber)	Maize rough dwarf (MRDV)
Dicranotropis hamata (Boheman)	Cereal tillering disease (CTDV), oat sterile dwarf (OSDV)
Javesella discolor (Boheman)	OSDV
J. dubia (Kirchbaum)	Arrhenatherum blue dwarf (ABDV), (European) wheat striate mosaic (E-WSMV), OSDV
J. obscurella (Boheman)	ABDV, E-WSMV, OSDV
J. pellucida (Fabricius)	ABDV, E-WSMV, Lolium enation, MRDV, OSDV, rice ragged stunt (RRSV)
Laodelphax striatella (Fallén)	Barley yellow striate mosaic, cereal tillering disease, northern cereal mosaic (NCMV), MRDV, oat pseudo-rosette[a,b], rice black-streak dwarf (RBSDV), rice stripe (RSV), wheat chlorotic streak
Muellerianella fairmairei (Perris)	NCMV
Nilaparvata lugens Stål	Rice grassy stunt, RRSV
Peregrinus maidis Ashmead	Maize mosaic, MRDV, maize sterile stunt (MSSV), maize stripe, maize stunting[a]
Perkinsiella saccharicida Kirkaldy	Sugarcane Fiji disease (SFDV)
P. vastatrix Breddin	SFDV
P. vitiensis Kirkaldy	SFDV
Sogatella furcifera Horváth	Pangola stunt
S. kolophon (Kirkaldy)	Digitaria striate mosaic, MSSV
S. longifurcifera Esaki & Ishihara	MSSV
S. vibix (Haupt)	MRDV
Sogatodes cubanus (Crawford)	(Rice) hoya blanca (HBV)
S. oryzicola (Muir)	HBV
Tarophagus proserpina (Kirkaldy)	Bobone disease
Terthron albovittatus (Matsumura)	NCMV, RSV
Unkanodes albifascia (Matsumura)	NCMV, RBSDV, RSV
U. sapporonus (Matsumura)	NCMV, RBSDV, RSV

[a]Virus has been associated with the vector or host plant, or both, but not confirmed as the etiologic agent.

[b]Disease etiology may involve both a virus and a mycoplasma-like organism.

for virus entering the hemocoele and exiting via the salivary system, a gradual decline in vector inoculativity when viruliferous insects are separated from a source of virus, and nontransstadiality. As with semipersistent, noncirculative aphid transmission, these characteristics are compatible with an ingestion-egestion transmission mechanism (Harris, 1977, 1980, 1981a). This hypothesis was confirmed by membrane-feeding studies on the feeding behavior of leafhopper vectors (Harris et al., 1981) and electron microscopic observations on the fate of MCDV in vectors (Harris, 1981c).

Detailed observations on the membrane feeding behavior of leafhoppers reveal that these insects, like aphids, usually egest material from the foregut one or more times during feeding (Harris et al., 1981). Initial periods of egestion are nearly always preceded by periods of prolonged ingestion. Periods of intermittent egestion sometimes last as long as 10 min, and insects often egest shortly before terminating probes. When egestion occurs, materials flow out of the maxillary food canal in the same steady manner in which they enter it during ingestion, indicating that the sucking pump of leafhoppers, like that of aphids (Harris and Bath, 1973), is able to function normally in either direction. The conditions under which these observations were made (Harris et al., 1981) are similar to those under which leafhoppers will feed and grow (Carter, 1927; Koyama, 1969; Mitsuhashi, 1979).

Electron microscopic observations on the fate of MCDV reveal numerous virus retention sites in viruliferous vector leafhoppers but not in non-virus-exposed vector controls or virus-exposed, nonvector leafhoppers such as Dalbulus maidis (De Long & Wolcott). Single- and multilayer aggregates of virions, as well as dense aggregates of virus particles in a matrix material, are adsorbed to the intima lining the cibarial pump, pharyngeal, and, especially, the esophageal regions of the gut. No virions are seen in association with the vector's stylets, in the gut beyond the esophageal valve, or in any other region or tissue of the vector. The ability of virus to accumulate and persist at retention sites in the foregut adequately explains the semipersistence and nontransstadiality of leafhopper retention of inoculativity.

The foregoing data suggest that the MCDV-leafhopper transmission system would be vulnerable to inhibition by oil (Harris, 1981c; Harris et al., 1981). It is known that oil can effectively prevent aphids from transmitting nonpersistent, semipersistent (beet yellows virus), and, possibly, even persistent (tomato yellows virus) viruses (Vanderveken, 1977; Simons and Zitter, 1980). The oil affects both the acquisition and inoculation phases of the transmission cycle, but how it does so is not known. Those adhering to the stylet-borne or "stylet-associated" view of noncirculative virus transmission propose a surface adherence hypothesis in which oil modifies the surface charge of the virion or stylets, or both, thus impeding virus adsorption to, or its elution from, the stylets. If this is a mode of action, it seems equally applicable to virus retained at adsorption sites in vectors' foreguts (Harris, 1978a, 1979, 1980). Aphids are known to ingest oil from oil-treated leaves (Vanderveken, 1973) and presumably leafhoppers would too.

Oil might also act by modifying the probing and feeding behavior that is responsible for transmission. The physico- and electrochemical properties of oils would enable them to insulate the sensory transduction system of a vector's feeding apparatus from, and to inhibit its interpretation of, the mechanical and phytochemical stimuli responsible for eliciting probing and feeding behavioral patterns such as anticlinal groove localization, sap sampling, deep probing, feeding-site localization, and prolonged feeding (Harris, 1977, 1978a, 1979, 1981d; Harris and Childress, 1981c). For example, ingested oil would presumably inhibit feeding by insulating the pharyngeal gustatory organ. This latter effect would be particularly important in semipersistent as well as persistent transmission in which vectors must ingest (acquisition) and eject (inoculation) larger amounts of virus-laden material to become infective and to inoculate virus to plants, respectively. Like the semipersistently transmitted, aphid-borne beet yellows virus, MCDV seems mainly limited to phloic tissues (Harris and Childress, 1981b, 1982). In any event, if oil acts on virus-vector or vector-plant interactions, the MCDV-leafhopper system seemed susceptible to inhibition on both counts and, therfore, deserving of testing in this regard (Harris, 1981c; Harris et al., 1981). This prediction was recently confirmed by a preliminary report of oil inhibiting MCDV transmission (D'Arcy and Nault, 1982).

Ingestion-egestion behavior might be involved in the transmission by leafhoppers of disease agents other than viruses; Pierce's disease agent of (PDA) of grapevines is a prime suspect (Harris, 1977, 1979, 1980). The transmission characteristics of PDA suggest that the vector-pathogen (bacterium) relationship is noncirculative. Retention of the xylem-restricted pathogen at adsorption sites in the foregut and inoculation via egestion seem most compatible with the characteristics of a brief or nonexistent latent period, prolonged retention of inoculativity by vectors, a broad vector range (low specificity), and persistent retention of inoculativity by adult insects. The PDA could thrive and possibly even multiply (hence, the persistence of adult vector inoculativity) in the foreguts of adult vectors while being bathed in a medium (xylem fluid) in which it is able to multiply (Harris, 1980, 1981a). The foregoing hypothesis is confirmed by data indicating that the vector does not retain inoculativity through ecdysis.

Ingestion-egestion behavior may be important in the transmission of pathogens by vectors other than aphids and leafhoppers (Harris, 1979, 1981a; Harris et al., 1981). A similar mechanism certainly seems operative in the transmission of tobra- and nepoviruses by dorylaimid nematodes (Taylor, 1980). Egestion seems typical of phytophagous Heteroptera as well. Egestion has been observed and electronically monitored in the case of the consperse stink bug, Euschistus conspersus Uhler (Hemiptera: Pentatomidae), especially at the ends of probes (Risk, 1969). Such feeding behavior could explain the ability of stink bugs to transmit the yeast-spot disease fungus, Nematospora coryli Peglion (Daugherty, 1967; Clarke and Wilde, 1970). This vector-pathogen relationship seems similar to that of PDA on the basis of its transmission characteristics. Egestion also seems a logical means by which the southern green stink bug, Nezara viridula (L.), might transfer fungi and bacteria to soybean infusion agar during feeding (Ragsdale and Larson, 1979).

Finally, evidence that certain blood-sucking arthropod vectors, e.g. biting flies and ticks, egest material during feeding, underscores the need to reevaluate and further elucidate how these vectors transmit pathogens to animals (Kloft, 1977).

MEMBRACIDAE

The only known instance of virus transmission by a treehopper involves Micrutalis malleifera Fowler and a virus, or presumed virus, that causes pseudo-curly-top disease in tomato (Table 1; Simons and Coe, 1958; Simons, 1962, 1980). Data relating to the vector transmission characteristics of the virus indicate that it is circulative. Whether it is propagative as well is not known. Attempts to localize virus or other pathogens in infected plant tissue or in the salivary glands of inoculative treehoppers have thus far proved negative (J. Richardson, personal communication in Simons, 1980).

DELPHACIDAE

Planthoppers have received far less attention from vector researchers than have aphids and leafhoppers. Even so, 13 genera and 23 vector species are recorded, and these are responsible for the transmission of 24 viruses (Table 1). The transmissions are all circulative, and most, if not all, of the viruses also appear to be propagative.

Propagative plant viruses are mainly found in the Reoviridae and Rhabdoviridae (Harris, 1979). Indeed, in the past, it was generally thought that multiplication of plant viruses in insect vectors was confined to viruses with 50-nm or larger diameters (Black, 1969). For some time this appeared to be the case; there were no unequivocal data to indicate that any of the small spherical or polyhedral viruses multiply in their vectors (Harris, 1979). In 1976, this belief was shattered by convincing evidence that the small, polyhedral, 28- to 30-nm oat blue dwarf virus (OBDV) multiplies in its leafhopper vector, Macrosteles fascifrons (Stål) (Banttari and Zeyen, 1976), making it the smallest, single-stranded RNA virus known to multiply in both plant and insect hosts. The 22- to 30-nm, isometric, ssRNA maize rayado fino virus also appears to multiply in its leafhopper vector, Dalbulus maidis (De Long & Wolcott) (Gámez et al., 1981). In keeping with the adage that records are meant to be broken are recent data suggesting that the even smaller, isometric, 20-nm rice grassy stunt virus multiplies in its planthopper vector, Nilaparvata lugens Stål (Shikata et al., 1980).

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