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Insect Transmission of Plant Viruses and Mycoplasmalike and Rickettsialike Organisms

Insect vectors are the most important means of spread of plant viruses and mycoplasmalike and rickettsialike organisms in nature. Few of these pathogens are sufficiently stable to be spread on their own; the vast majority require protection during dispersal. Plant material may provide protection, as in the case of vegetative propagation or seed transmission. Often, the pathogen is harbored within a vector and protected from the environment while being transported through time and across space. Fungi, mites, or nematodes serve as vectors in a few cases, but most of the time the vector is an insect. Insects not only protect the pathogen but also create feeding wounds that serve as entry points into susceptible plants. The evolutionary development of the close and complex relationships among plant hosts, insect vectors, and these pathogens probably required aeons. Some of the pathogens, for example, multiply within their insect vectors and perhaps were "insect pathogens" before they became "plant pathogens."

Plant mycoplasmas and rickettsias are small, fastidious bacteria morphologically similar to the Mycoplasmatales and Rickettsiales that infect animals. Until their relationship to these groups is proved, however, they are called mycoplasmalike organisms (MLOs) and rickettsialike organisms (RLOs). The plant diseases incited by MLOs and RLOs were thought for many years to be caused by viruses because of similarities in symptomatology and vector transmission, their graft transmissibility, and the failure to detect a visible pathogen.

Clues for finding a vector of a particular plant virus, MLO, or RLO disease may be obtained by studying the pattern of disease incidence in both time and space. For example, seedborne viruses appear very early in the growing season and viruses transmitted by fungi or nematodes tend to occur in the same locations year after year and to spread slowly. Diseases spread by insects may follow one of several patterns, depending largely on the source of the pathogen. If the source is within the crop, disease is likely to spread in patches around each focus of infection. If the source is outside but close to the crop, a spatial gradient of infection is likely, ie, plants close to the source are more likely to become infected than those farther away. If the pathogen source is distant from the crop, no infection gradient may be seen. In northern Illinois, for example, maize dwarf mosaic virus infection of sweet

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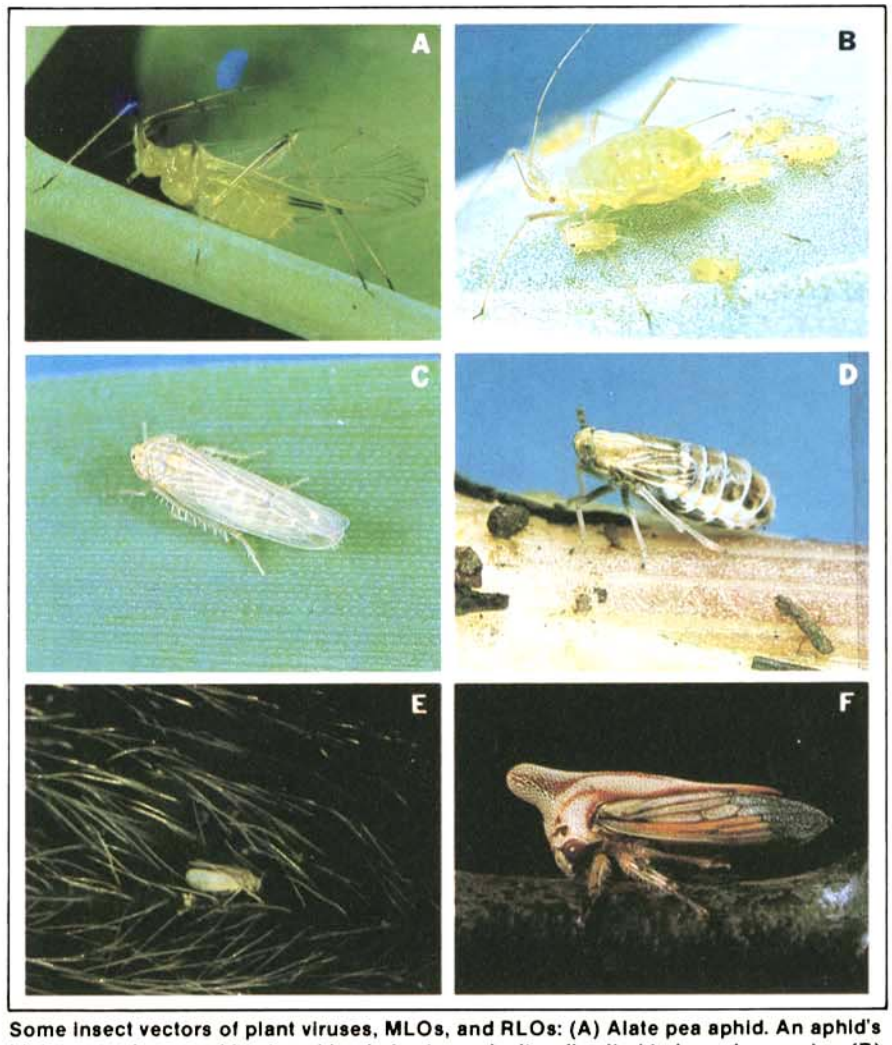

Some insect vectors of plant viruses, MLOs, and RLOs: (A) Alate pea aphid. An aphid's biology, ecology, and host-seeking behavior make it well suited to be a virus vector. (B) Apterous pea aphid giving birth to first instar nymphs. Aphids are parthenogenetic and viviparous, reproductive strategies allowing for rapid population buildup. (C) Mexican corn leafhopper, capable of transmitting a mycoplasma, a spiroplasma, and a virus. The deltocephaline leafhoppers are effective vectors of phloem-inhabiting plant pathogens. (D) Planthopper. Among the Auchenorrhyncha, the delphacid planthoppers are second in importance only to the leafhoppers as vectors. (E) Whitefly (courtesy Julio Bird). Whiteflies are important vectors of plant pathogens in tropical and subtropical regions. (F) Treehopper (courtesy Tom Wood). These species, abundant in the tropics, are potentially important vectors of plant pathogens.

Table 1. Distribution of plant pathogens among insect vectors

Order	Phytophagous species	Type of adult mouthparts	Viruses transmitted (no.)	MLOs and RLOs transmitted (no.)
Paurometabola				
Orthoptera	Grasshoppers, locusts, crickets	Chewing	2	0
Dermaptera	Earwigs	Chewing	1	0
Thysanoptera	Thrips	Lacerating-sucking	1	0
Hemiptera	True bugs	Piercing-sucking	3	2
Homoptera	(see Table 2)	Piercing-sucking	253	45
Holometabola				
Coleoptera	Beetles	Chewing	30	0
Lepidoptera	Butterflies, moths	Sucking	3	0
Diptera	Flies	Sponging-lapping	2	0
Hymenoptera	Ants, bees, wasps	Chewing	0	0

Table 2. Distribution of plant pathogens among Homopteran vectors

Suborder Family	Common name	Species described (no.)	Vector species (no.)	Viruses transmitted (no.)	MLOs and RLOs transmitted (no.)
Auchenorrhyncha					
Cicadidae	Cicada	3,200	0	0	0
Membracidae	Treehopper	4,500	1	1	0
Cercopidae	Spittlebug	3,600	10	1	2
Cicadellidae	Leafhopper	40,000	130	38	39
Fulgoroidea[a]	Planthopper	9,200	21	18	1
Sternorrhyncha					
Psyllidae	Psyllid	2,000	6	0	3
Aleyrodidae	Whitefly	1,200	3	10	0
Aphididae	Aphid	4,000	192	169	0
Pseudococcidae	Mealybug	6,000	19	4	0

[a]Superfamily includes the families Cixiidae, Delphacidae, and Flatidae.

corn fields follows no apparent gradient; rather, diseased plants appear randomly. Probably flights of alate (winged) aphid vectors carry the virus in from a distant source.

The rate of spread of insect-vectored viruses, MLOs, and RLOs also varies. Disease spread may be very slow if environmental conditions do not favor vector multiplication and movement or virus multiplication in host plants. Aerial transmission by insects can be extremely rapid, however, with entire fields becoming infected within a few days. Because other known means of virus transmission require considerable time, insect vectors should always be considered when the incidence of a virus, MLO, or RLO disease increases rapidly.

Types of Insect Vectors

More than 1.1 million insects have been described since Carolus Linnaeus penned the first Latin binomial for an insect over 200 years ago. (It is estimated that 1–2 million insect species remain undiscovered and undescribed.) Perhaps half of all described and undescribed species are plant feeders and potential vectors of plant pathogens. Despite this, insects from only one order, the Homoptera, stand out as "successful" vectors (Table 1). What sets the Homoptera apart from other insect groups?

Unlike the Homoptera, phytophagous insects from the holometabolous orders have immature stages that differ greatly from the adults, often with different habitats and feeding habits. In the phytophagous Lepidoptera, Diptera, and Hymenoptera, the larvae are plant feeders and the adults usually are nectar and pollen feeders or may have nonfunctional mouthparts. The Coleoptera, the most successful vectors of the holometabolous insects, are an exception, with the adults of many species being plant feeders. This is consistent with the observation that the adult stage of the insect is most responsible for transmission of plant pathogens.

The similarity in feeding behavior and other habits between the nymphal and adult stages of the paurometabolous Homoptera may explain, in part, their success as virus vectors. Only the closely related Hemiptera share the highly adapted piercing-sucking mouthparts. The two orders differ, however, in attachment of the beak that contains the piercing stylets. In the Hemiptera, the beak or rostrum arises from the front part of the head. This forward placement of the rostrum has allowed development of predatory forms; perhaps 25% of the species are predaceous, with the remaining species phytophagous. In the Homoptera, the rostrum arises from the posterior part of the head, and all members of the order are phytophagous. Unlike insects with chewing mouthparts, the phytophagous Hemiptera and Homoptera can selectively feed in the mesophyll, phloem, or xylem, making them ideal vectors for pathogens residing in these tissues. It is still surprising that only five plant pathogens are known to be transmitted by the Hemiptera, compared with nearly 300 by the Homoptera. We suggest a more thorough examination of the Hemiptera as potential vectors of plant viruses and other pathogens.

Even within the Homoptera, vectors are not distributed evenly among the families (Table 2). In the suborder Auchenorrhyncha, the leafhoppers and planthoppers emerge as dominant vectors. Members of both these insect families are abundant in temperate regions and frequently inhabit cultivated crops. They are, therefore, better studied as vectors than their cicada, treehopper, and spittlebug relatives, whose species are more common in the tropics. The cicadas represent a special case among the Homoptera with their soil-inhabiting immature stages. This habit may contribute to their nonvector status as much as inattention to the group by vector specialists.

Aphids dominate the suborder Sternorrhyncha as vectors. They are as well known for their ability to vector viruses as they are for being pests of cultivated crops. Most species have a complex life cycle involving bisexual and parthenogenetic generations, winged and wingless generations, and some species have a regular alternation of food plants. Parthenogenesis is coupled with birth of active, first instar nymphs (viviparity) during summer generations. This reproductive strategy, frequently involving a sequence of food plants, and a feeding behavior that includes "test probing" of the leaf epidermis make them ideal plant virus vectors. The other Sternorrhyncha—psyllids, whiteflies, and coccids, including mealybugs—do not match the biotic potential or dispersive capacity of aphids. Although their theoretical effectiveness as vectors of plant pathogens is thus reduced, the importance of these insects as vectors may be far greater than currently recognized. Many species are found in tropical zones of the world and have not been extensively tested as vectors.

Undoubtedly, many more Homopteran-transmitted pathogens and vector species will be described. Fewer than 0.5% of nearly 77,000 described Homopteran species have been identified as vectors of

plant pathogens. Even in the best studied group, the aphids, only 300 of 4,000 species have been tested as vectors. As agricultural production intensifies and diversifies in tropical regions of the world, we expect the number of known pathogens and Homopteran vectors to increase many times.

Transmission Patterns

Most cases of virus transmission by insects that do not have piercing-sucking mouthparts appear to be mechanical rather than biological. These are probably analogous to the transmission of a few highly concentrated and stable plant viruses, such as tobacco mosaic, on human hands and tools. The exception to this is the Coleoptera. We cannot explain why beetles transmit some stable viruses that infect plants on which they feed, such as southern bean mosaic virus, but not others equally or more stable, such as the cowpea strain of tobacco mosaic virus. As yet unknown biological factors must be determining this specificity.

The three patterns of biological transmission by Homopteran vectors are nonpersistent or styletborne, semipersistent, and persistent or circulative.

Nonpersistent transmission. More than 100 plant viruses are transmitted in a nonpersistent manner. These viruses are rapidly acquired during vector probing of virus-infected plants, often in less than a minute. The insect can inoculate the virus without delay into another plant equally rapidly. Transmission can thus be accomplished in an extremely short time. In general, the vector retains the virus for only a few minutes or hours, which is why this type of transmission was called "nonpersistent" by Watson and Roberts (14). The transmitted virus does not enter the midgut of the vector and therefore is lost whenever the vector molts. Transmissible virus is believed to be confined to the vector's stylets and/or foregut, which led to the term "styletborne" coined by Kennedy, Day, and Eastop (6).

Currently, an ingestion-egestion hypothesis is proposed to explain nonpersistent transmission. Virus ingested during host sap sampling is later egested or regurgitated from the foregut during probing or feeding. When vectors are removed from their host plant and starved for several hours before being placed on a virus-infected plant, efficiency of virus acquisition is increased. The starvation period changes vector behavior; the vector makes many short probes after a period off a plant, which increases the chance of acquiring virus.

The question has arisen as to whether our methods of testing the retention period of nonpersistently transmitted viruses has given us a false idea of their life span in the vector. Retention times are generally measured both on the host, while the vector is able to probe and feed, and off the host, typically in a petri dish. Even while in a petri dish, however, the vector attempts to probe as one method of testing the environment. The virus may be lost during this process. In the natural situation, the vector is usually airborne during movement from plant to plant, sometimes over long distances. There is nothing on which it can probe, and therefore virus may be retained longer. Recently, researchers at the University of Minnesota found that maize dwarf mosaic virus can be retained longer than a day by aphids anesthetized with nitrogen or immobilized on ice after virus acquisition (1). The longest previously reported virus retention time in an aphid vector was 6 hours, and the typical retention time was 1 or 2 hours. Experimental conditions, however, do not reproduce the natural situation.

In general, nonpersistently transmitted viruses are stable and occur in relatively high concentration in epidermal cells of their plant hosts. Many are long flexuous rods, such as those in the potato virus Y group. Practically all (about 98%) nonpersistent transmission is by aphids.

Semipersistent transmission. A few plant viruses are transmitted in a manner that Sylvester termed semipersistent (12). Acquisition and inoculation require longer periods than for nonpersistent transmission, usually several minutes to an hour. The virus is also retained longer, although still not through molts. The longer a vector is allowed to feed on a source plant, the longer it will be able to inoculate the virus. This is not true for nonpersistent transmission, in which acquisition efficiency declines during long feeds. The viruses transmitted in a semipersistent manner are a heterogeneous group; for example, beet yellows and strawberry vein banding viruses are transmitted by aphids and rice tungro and maize chlorotic dwarf viruses by leafhoppers.

Persistent transmission. More than 80 plant viruses and all plant MLOs and RLOs are transmitted by several different vector taxa in a persistent or circulative manner. The pathogens are acquired slowly from the diseased plant, usually over hours to days. A similarly lengthy period is required for efficient inoculation. These pathogens usually have a latent period in the vector, that is, a period of time after acquisition during which no transmission occurs. The latent period can be hours, days, or weeks. The pathogen circulates within the body of the vector, hence Black's term, "circulative" (2). These pathogens enter the body cavity via the midgut and thus are retained through molts.

"Circulative-nonpropagative" has been used to describe pathogens that do not multiply in the vector, and "circulative-propagative" to describe pathogens that do; these terms are often shortened to circulative and propagative, respectively. Watson and Roberts' term "persistent" covers both types of transmission and refers to the fact that these pathogens can be retained in their vectors for long periods of time (14). Circulative-nonpropagative pathogens have shorter latent periods (a few hours or days) in their vectors than circulative-propagative ones (several days or weeks). A pathogen that multiplies is often retained for the life of the vector and is sometimes passed to progeny through the egg (transovarial passage).

Many pathogens transmitted in a persistent manner are confined to the phloem or xylem of their plant hosts and therefore cannot be transmitted mechanically. The length of time a vector needs to reach a vascular bundle with its mouthparts helps explain why aquisition and inoculation of these viruses require more time than nonpersistently transmitted viruses. A second, more important factor is the time required for the virus, MLO, or RLO to enter the gut, pass into the body cavity, perhaps multiply, enter the salivary glands, and be ejected during salivation associated with probing or feeding.

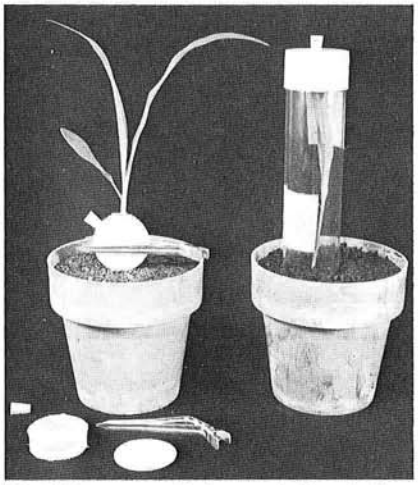

Fig. 1. Cages used in transmission studies: (Left) Clip-on cage constructed from a small plastic petri dish covered on both sides with fine mesh fabric, wax-impregnated cardboard lid, and hairclip. (Right) Whole plant cage constructed from a butyrate tube, fabric-covered vent holes, and plastic top with corked hole for introduction of insects.

The degree of pathogen-vector specificity is generally high in cases of persistent transmission, probably because of the intimate pathogen-vector interaction and the length of time the vector must feed on the plant to acquire the pathogen. Some viruses transmitted in this manner, such as the plant rhabdoviruses, multiply in their vectors, while others, such as the luteoviruses, do not.

Almost all (about 97%) known cases of virus transmission by leafhoppers are persistent, as are all those by planthoppers and whiteflies. All the MLOs studied so far are thought to multiply in their leafhopper and planthopper vectors. Clover clubleaf and Pierce's disease RLOs have been shown to multiply in their leafhopper vectors, but little is known about the vector relationships of other plant RLOs. Pathogen multiplication has been proved in only a few vectors; in most cases, evidence has not been conclusive.

Either of the two major types of transmission, nonpersistent or persistent, can result in an explosive epidemic. Nonpersistent transmission favors rapid spread of a pathogen from infected to nearby healthy plants but is less efficient for transporting viruses over a long distance. Usually a vector can inoculate only one or two plants before it must reacquire the pathogen by probing or feeding on an infected plant. Persistent transmission allows vectors to inoculate many plants without revisiting a source and thus spread a pathogen over considerable distances, even hundreds of miles.

Testing for Insect Transmission

When disease spread patterns or other evidence suggests insect transmission, the search for the vector begins. Certain bits of information can narrow the search. If the pathogen is mechanically transmissible, a leafhopper, planthopper, or whitefly vector is unlikely; aphids, beetles, or such noninsect vectors as eriophyid mites and nematodes are more likely candidates. Viruses occurring in high concentrations in host tissues often have beetle or nematode vectors. Knowledge of host ranges, symptoms, and serologic relatedness to other viruses can lead to rapid determination of insect vectors.

Information provided by electron microscopy also can be helpful. Appearance and location of viruses, MLOs, and RLOs in diseased tissues can help pinpoint vector taxa. The xylem-inhabiting RLOs are known to be transmitted only by the xylem-feeding leafhoppers in the subfamily Cicadellinae and by spittlebugs. Leafhoppers are the principal vectors of the mycoplasmas but other Homopteran vectors have been reported (Table 2). The phloem-restricted viruses are usually transmitted by the Homoptera; those with small isometric particles are often aphidborne, but a few leafhopper-transmitted viruses with this morphology are known. The rhabdoviruses are most often transmitted by leafhoppers and planthoppers, but aphids too are involved. The aphids are the principal vectors of viruses with flexuous rod-shaped particles, whereas very few such viruses are transmitted by the auchenorrhynchous Homopterans.

When searching for an insect vector, the first impulse is to collect from the infected host in the field. This is a good strategy, particularly with pathogens restricted to vascular tissue and requiring prolonged feeding by the vector for

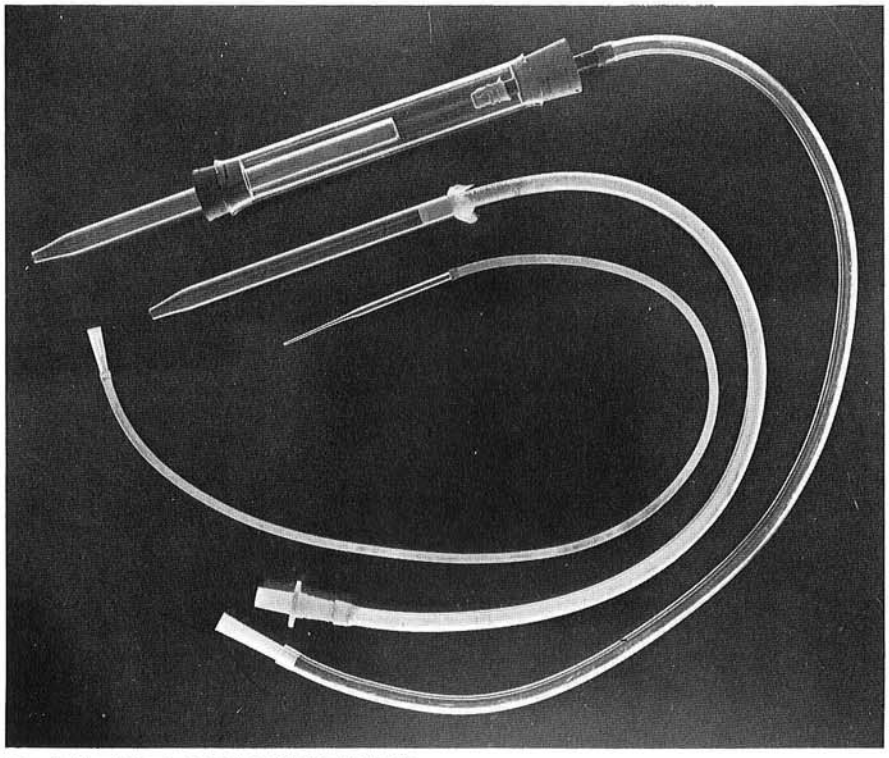

Fig. 2. Aspirators used to pick up vectors.

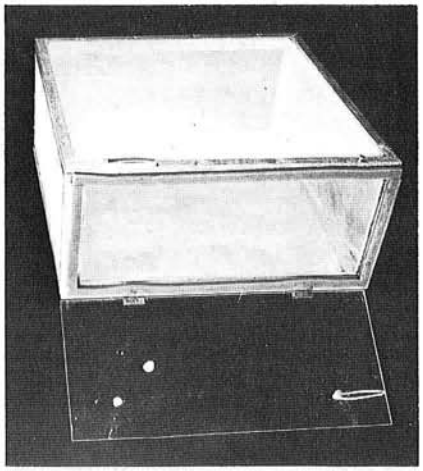

Fig. 3. Rearing cage constructed from an aluminum frame covered with Dacron organdy and fitted with a Plexiglas door.

acquisition and inoculation. Their vectors can often be found colonizing the diseased host. Other sources of vectors can be found in nearby crops and wild or weedy plants. Frequently, the vector feeds only occasionally on the diseased crop being studied and is found more readily colonizing another plant species.

Potential vectors of a plant pathogen should be given inoculation access periods on susceptible test plants for periods ranging from a few minutes to several days. Leaf or whole-plant cages can be used for this purpose (Fig. 1). Relatively inactive vectors, such as apterous (wingless) aphids, may be handled with a fine, moistened brush; more active alate insects require the use of aspirators (Fig. 2).

Another strategy is to test field-collected or laboratory- or greenhouse-reared insects as vectors on infected plants or plant parts. Again, access time on infected plants and test plants should vary. Because a number of plant pathogens must undergo an incubation period of several days or weeks before their vectors can transmit them, insects should be placed on holding plants after access to infected plants and before placement on test plants. It is advisable to use large numbers of candidate insects in the search for potential vectors. If the pathogen titer in field-collected plants is low, the percentage of vectors becoming inoculative will also be low. The ultimate choice of insects to be used in the vector search depends on the available information on pathogen characteristics and the disease ecosystem. The investigator also should throw in a large dose of intuition and hope for a measure of good fortune.

Rearing the identified vector is not always easy. Many insects will not adapt well to the restraints and environment of a rearing cage (Fig. 3). Although artificial diets have been developed for some species, rearing vectors on their plant hosts is usually much easier. The feeding habits of the vector determine host selection. Many insects are monophagous, offering no choice. Selecting a host for a vector with a broader range includes finding a plant 1) easy to grow from seed or other plant parts, 2) on which the vector will readily lay its eggs or deposit its nymphs, and 3) that survives well when fed on by large numbers of developing individuals. Another consideration is selecting a host that is immune to the plant pathogen being studied, to prevent accidental perpetuation of the plant pathogen in the "pathogen-free" vector colony.

Finally, in vector rearing there is no substitution for a thorough understanding of the insect's biology and ecology. If this information is not available in the literature, additional research must be conducted. Temperature and photoperiod are the two most critical factors in successful rearing of a vector. When these and other environmental factors are properly balanced, a large supply of rapidly developing and vigorous insects can be made available for experimental transmission of plant pathogens.

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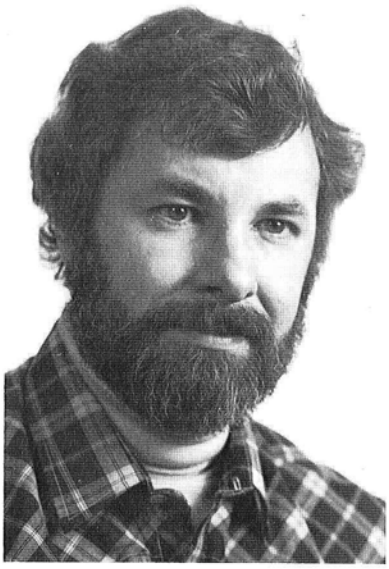

Lowell R. Nault

Dr. Nault is professor of entomology and professor of plant pathology at the Ohio Agricultural Research and Development Center and Ohio State University. For the past 16 years he has studied maize pathogens transmitted by aphids, leafhoppers, planthoppers, beetles, and eriophyid mites. He is known for his contributions to vector biology, ecology, and behavior, and particularly for his pioneering work with the alarm pheromones of aphids.

Control

Basic knowledge of the complex relationships among pathogen, vector, and host plant is of paramount importance to successful disease control. The kind and source of the vector, the vector's means of transmitting the pathogen, and the effect of environment on the vector must all be determined.

Many methods, including using clean seed or planting stock, roguing infected plants, and incorporating host resistance to the pathogen, have been used to control insect-vectored virus, MLO, and RLO diseases. Some methods are unique to control of insect-vectored pathogens, and success often depends on the transmission pattern of the disease instead of the pathogen-vector-host combination.

Some vectors of plant pathogens can simply be avoided by adjusting cultural practices. For example, early planting may allow crops to develop beyond the period of greatest susceptibility to a pathogen before vectors arrive. When pathogen and vectors move from one crop cycle into the next, and are not harbored in alternate hosts, disease can be controlled by breaking the cropping sequence. All growers in an area must cooperate, however, for this tactic to succeed.

Crops also can be planted in areas where vectors are rare or absent during the susceptible period of plant growth. Seed potatoes are traditionally grown in cool regions, such as the northern United States, where aphid vectors arrive too late for the viruses they carry to become established and spread significantly within the crop. Changing the time or place of planting is effective in particular situations for any type of pathogen transmission—nonpersistent, semipersistent, or persistent.

Because nonpersistent transmission is a rapid process, many control procedures are designed to keep arthropod vectors from alighting on the susceptible crop. One such cultural practice is to plant a barrier crop around the edge of the field; vectors are attracted to and/or trapped by the barrier and probe enough to lose a significant amount of their virus charge. Another cultural method is to place a reflective mulch in plant rows; virus transmission has been effectively controlled in several crops by covering 50% of the ground area with aluminum or white plastic mulch (11). Winged vectors are repelled by light reflected off the

mulch, and the number that alight can be reduced by 90% or more. This may delay the virus epidemic many weeks and greatly increase yield. Mulching materials and labor are expensive, however, and this method is economically feasible only for row crops of high value.

A recently emphasized means of controlling nonpersistent transmission is to spray plants with oil (10). The mechanism by which oil prevents nonpersistent transmission is not understood; the effect may be on acquisition, inoculation, or vector behavior, or any combination of these. Coverage must be excellent to be effective. Therefore, sprays are required at 3- to 7-day intervals during a growing season, and this also becomes expensive.

Control of persistently transmitted plant viruses, MLOs, and RLOs usually involves insecticides. Too slow-acting to control nonpersistent transmission, insecticides are effective against the slower persistent process. Crops must be protected whenever vectors are present. Nevertheless, insecticidal control is never complete because not all vectors can be eliminated before transmitting the pathogen to healthy plants. This is especially true if insects have fed on infected plants before entering the crop. The cost of in-crop insecticides can be reduced by knowing when vectors are likely to arrive and applying only necessary sprays. The path in the south central United States of the aster leafhopper, vector of the aster yellows mycoplasma, has been monitored every spring for many years to predict its arrival in the north central states; this prediction allows growers to avoid unnecessary sprays and thereby save both time and money. In some instances, spraying noncultivated hosts of a pathogen and/or its vector in areas surrounding susceptible crops prevents movement of infective insects into the crop.

The methods usually most effective for control of nonpersistent or persistent transmission of viruses have been shown experimentally to be effective against semipersistent transmission. For example, oil lowers transmission of maize chlorotic dwarf virus, while insecticides reduce spread of rice tungro virus.

Among control measures that may have potential for the future are incorporating resistance to vectors into plant hosts and using pheromones to control vector behavior. Such methods have the advantage of being harmless to man and the environment, but their potential probably will not be realized for several years.

Summing Up

In over 80 years of research on insects as vectors of plant viruses, MLOs, and RLOs, many discoveries have been made but many questions remain unanswered. These include questions concerning the mechanisms of pathogen-vector specificity for all types of transmission. Why, for example, is cauliflower mosaic virus transmitted nonpersistently by some aphids and semipersistently by others? Why can some insects efficiently transmit one pathogen but not another, very similar one? In a relatively short space we have tried to present an introduction to a broad and diverse topic. To do this we often have had to generalize. If you intend to work on an insect-transmitted pathogen we strongly suggest that you seek more detailed knowledge from such references as are listed below (3–5,7–9,13).

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