Insects as Vectors of Disease Agents

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INTRODUCTION

Vectors are organisms that can introduce a pathogen such as a bacterium or virus into a plant to cause an infection. Insects, mites, and nematode vectors focus the movement of plant pathogens among immobile plants. Many insects or other arthropods may contain plant pathogens but cannot transmit these to plants and thus are not vectors. Some of our most important plant diseases require mobile vectors. Almost all plant viruses and all wall-free, plant pathogenic bacteria known as mollicutes have recognized or suspected vectors. See elsewhere for insect vector transmission of bacterial plant pathogens.

Much research on vector transmission seeks to understand the transmission process so as to explain why only certain kinds of insects or mites can serve as vectors and to identify what factors are required for transmission.[1] Because insecticides applied to kill vectors frequently fail to control the diseases caused by the vector-borne pathogens, a good understanding of the relationships between vectors and the pathogens that they transmit is important.

Vector transmission processes are usually complex, even for the seemingly simple mechanical transfer of plant viruses to plants on the tips of vectors' stylet-like mouthparts (similar to a hypodermic needle) during feeding. In many other cases, the plant parasites transmitted by insect vectors must multiply and circulate throughout the body of the vector to be transmitted. The most fundamental characteristic by which to classify or categorize vector transmission is that of transmission efficiency (also called vector competence), or how often a vector transmits a pathogen over time or per transmission opportunity. Transmission efficiency can increase or decrease over time after a vector first acquires a pathogen, usually by feeding, but some pathogens are transmitted from a mother vector to her offspring via her eggs or embryos. Generally, vector acquisition of pathogens increases with time spent feeding on infected plant sources of the pathogen. Transmission is called nonpersistent if the rate of transmission drops to near zero within a short time (hours). Nonpersistent transmission of viruses also differs from other types of vector–pathogen relationships in that acquisition generally decreases rather than increases with sustained feeding on infected plants. Semipersistent transmission persists for, at most, a few days after acquisition. Persistent transmission describes situations in which the vector can transmit over many days, in some cases, for weeks or months.

LATENT PERIOD

Vectors that increase their transmission rates over time have a latent period: the time between a vector's acquisition of the pathogen and its first transmission to plants. Some vectors never transmit a pathogen until days or weeks after they first acquire it. In contrast to these long latent periods, some vectors need no latent period; transmission can occur immediately after acquisition. (See Table 1 for examples.)

The nonpersistent transmission of viruses by aphids illustrates the importance of how vector transmission characteristics contribute to the spread of plant disease and why some control strategies for these viruses differ from those for other aphid-transmitted viruses. Potato virus Y (PVY) and other potyviruses are transmitted by a wide variety of aphids (family Aphididae; Fig. 1) in a nonpersistent manner (relatively low vector specificity). The optimum time for an aphid to acquire PVY is after only a few minutes of feeding. The most convincing experimental evidence points to the tips of the vector stylets (Fig. 2) as the critical region where the virus is transferred from vector to plant during feeding. A bridging polypeptide molecule links virus particles to the aphid's stylet tips.[2] A virus can genetically code for its own linking molecule (''helper factor'') or provide a helper factor to aid the aphid transmission of another virus. How the virus detaches from the vector mouthparts is not understood.[3] The nonpersistent nature of the transmission of PVY fits in well with the flight behavior of its aphid vectors to promote virus spread in crops. Alighting aphids typically make a few probes on the first plant on which

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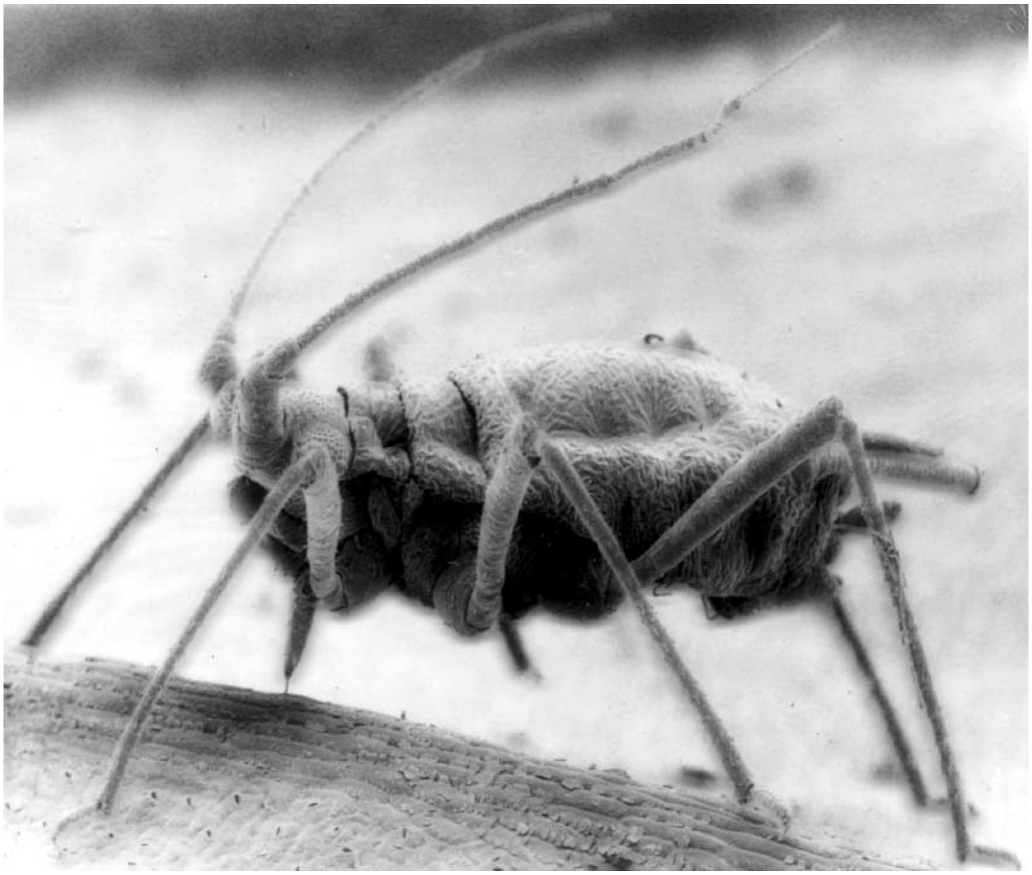

Fig. 1 The slender needlelike mouthparts of the feeding aphid barely protrude from the larger surrounding sheath touching the plant surface. (Photo by and courtesy of Marvin Kinsey.)

they land and then fly short distances to other plants until they settle to feed continuously and reproduce. Because the aphids rapidly lose infectivity, they do not often disperse the virus over long distances. Most virus spread in such cases is from plant to plant within a field, making sanitation to eliminate seed transmission or other ways that introduces virus into a crop a key control method.[4] The aphid vectors' rapid transmission of virus without a latent period and during exploratory feeding probes makes reducing of virus spread by killing incoming aphids with insecticides ineffective.

PLANT VIRUSES

Virus Vector Groups

Most vectors of plant viruses are sucking insects in the order Homoptera[5] (considered the order Hemiptera by most recent classifications). Their small stylets allow vectors to introduce virus into plant cells or vascular tissues with minimal feeding damage. Aphids (Aphididae) transmit the greatest variety of plant viruses. Next in importance are the whiteflies (Aleyrodidae), followed by the leafhoppers (Cicadellidae) and planthoppers (Fulgoroidea). Some viruses have mealybug vectors (Pseudococcidae), and various other hemipteran families have virus vector species. Only a few viruses are transmitted by thrips (Order Thysanoptera), but their economic impact is internationally important. However, some important viruses require leaf beetle (Chrysomelidae) or weevil (Curculionidae) vectors. Viruses transmitted by beetles (order Coleoptera) seem to be best able to withstand, perhaps even require, the severe tissue damage caused by beetle vector feeding that inoculates the virus into plants. The microscopic bud or gall mites in the family Eriophyidae are the most important of the noninsect arthropods that are virus vectors.

Persistent Transmission of Viruses and Other Pathogens

Numerous viruses and other disease agents are transmitted by an infectious vector for many days or even weeks. For example, the beet curly top virus (BCTV)

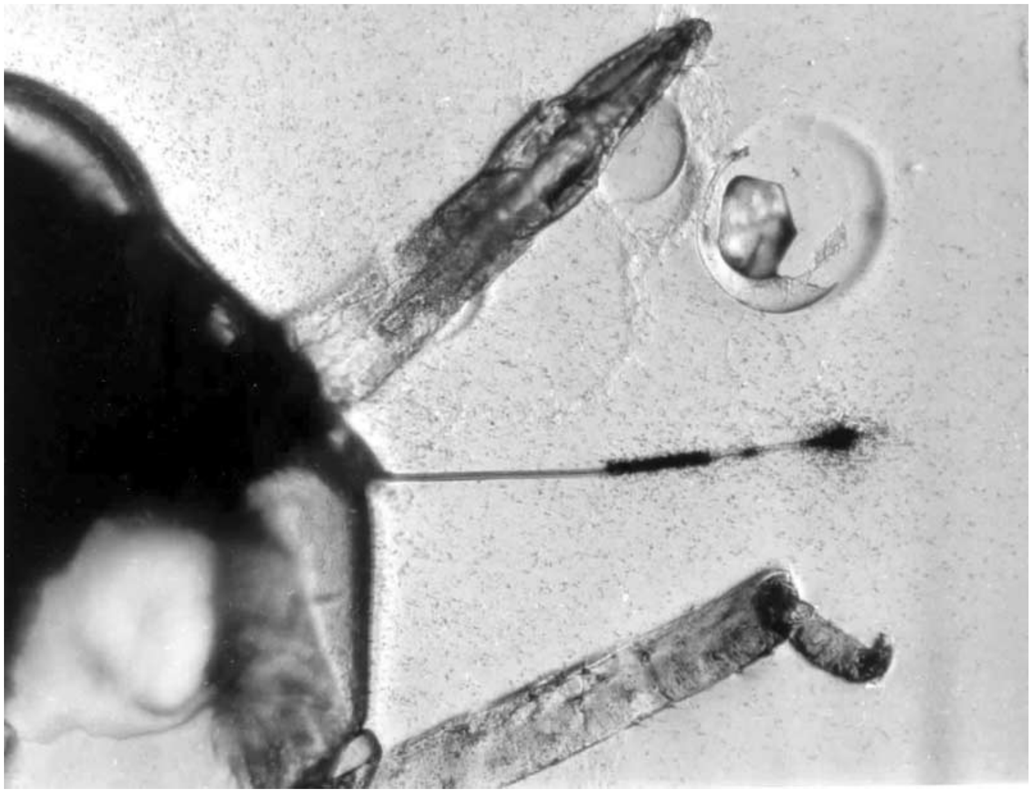

Fig. 2 X-rays capture the location of radioactive isotope-labeled virus (cluster of tiny black spots) on the very slender probing stylets of an aphid. (Photo by and courtesy of R.Y. Wang.)

has only one known vector, the beet leafhopper (*Circulifer tenellus*).[5] Infectious beet leafhoppers transmit the virus after a latent period of only a few hours and continue to transmit for days to weeks. The length of time that they continue to transmit depends on how long they feed on a virus-infected plant to acquire this geminivirus. Beet curly top virus is an example of a persistently transmitted virus that is circulative but does not multiply within the vector.[5] This virus also requires a longer feeding period for vector transmission. Like BCTV, the aphid-borne, persistently transmitted viruses that cause the internationally important diseases barley yellow dwarf and potato leafroll (luteoviruses) can be controlled by effectively timed applications of insecticide that kill aphids shortly after they fly into the crop.[4] Most lengthy latent periods result from the requirement of the pathogens to multiply within the vector to attain the numbers needed to complete the vector transmission process by reaching the salivary glands in sufficient numbers. Some viruses and bacteria multiply within numerous types of organs and tissues within the vector that probably are not required for transmission, and a consequence is that some of these plant pathogens are harmful to the vector. Reoviruses (rice dwarf, for example) multiply within both their insect vectors and plant hosts. Multiplication and circulation of the pathogens within the body cavity (hemocoel) of the vector insures that the pathogen will remain within the vector after molts that occur as the vector develops. Nonpersistently or semipersistently transmitted viruses are no longer transmitted once the vector has molted its exoskeleton.

NONVIRAL PATHOGENS

Vectors and Fungi

Insect feeding damage can cause wounds that promote the invasion of fungi that damage plants or their fruit.[5] A variety of sucking insects that feed on fruits can introduce the fungus *Nematospora corylii*, which causes yeast spot disease of bean, coffee, cotton, and a variety of other crops. The feeding of a sucking insect, the grape phylloxera, causes lesions on the roots of grapevines that are invaded by soil fungi that deteriorate the roots.[6]

Dutch elm disease is a representative example of a disease caused by a beetle-transmitted fungus, *Ophiostoma ulmi*. The fungus colonizes the wood of living elms or recently killed trees or cut logs, which are also where the bark beetle larvae develop beneath the elms' bark. Fungal spores of *O. ulmi* are sticky and attach to the newly emerging adult bark beetles. After flying to other elms, the beetles introduce the spores into feeding wounds on small twigs or into the tunnels excavated under elm bark by the bark beetles for egg laying.[5] The fungus spreads into the tree's vascular system. Elms weakened by the Dutch elm disease are more attractive for new beetle attacks. Control requires vigilant sanitary measures of quickly removing and destroying diseased elms to eliminate the fungus and reduce the numbers of developing bark beetles.[7]

Trypanosomes and Nematodes

Sucking insects can also vector trypanosomes (flagellated protozoa) that infect various plants, causing especially serious diseases of palms and coffee. Other insect-vectored trypanosomes cause mild or symptomless infections of milkweeds and tomatoes.[8] Wood-boring beetles (Cerambycidae) serve as vectors of nematodes that cause pine wilt disease. Immature nematodes multiply within plant tissues and enter the spiracles of the newly molted adult beetles. The nematodes crawl out of their beetle transporters after the beetles have flown to other trees and excavated egg-laying chambers in the trees' trunks to lay eggs (Table 1).

CONTROL OF PLANT DISEASES CAUSED BY VECTOR-BORNE PATHOGENS

The principal methods to control crop disease spread by vectors limit vector acquisition of the pathogen or prevent infective vectors from transmitting to susceptible crops. The impact of insecticides for vector control on disease spread depends on the vector transmission characteristics of the pathogen, as previously discussed. Sanitation is most often used to prevent vector acquisition. This requires the removal of diseased plants or insuring that new plants are free of the targeted pathogen by using certified propagating materials. Physical isolation of crops from exposure to vectors can be used in greenhouses or by growing crops in regions where the vector populations are very low. Varying planting dates can be used to avoid peak periods of vector activity if these can be reliably predicted and do not cause unacceptable losses in yields or quality. Using resistant varieties of plants is a highly effective control if genetic resistance is available. Molecular methods of producing new varieties promise to increase the availability of resistant

Table 1 Representative examples of diseases caused by vector-borne pathogens

Type of pathogen	Vector	Type of transmission (see text for explanation)
Virus		
Lettuce mosaic potyvirus	Aphids (many species)	Nonpersistent
Barley yellow dwarf luteovirus	Aphids (few species)	Persistent days to weeks, circulative, not propagative in vector
Lettuce necrotic yellows baculovirus	Aphids (many species)	Persistent, circulative, propagative in vector
Maize rough dwarf reovirus	Planthoppers (very few spp.)	Persistent, circulative, propagative, and transovarial in vector
Maize streak geminivirus	Leafhoppers (*Cicadulina* spp.)	Persistent, circulative, nonpropagative
Southern bean mosaic sobemovirus	Leaf beetles (Chrysomelidae)	Semipersistent to persistent, noncirculative (?)
Bacteria		
Xylella fastidiosa (numerous diseases)	Xylem sap-feeders (sucking insects in several families)	Noncirculative but persistent, propagative in vector
Aster yellows phytoplasma	Leafhoppers (several spp.)	Persistent, circulative, propagative
Trypanosomes		
Hartrot of palm	Shield bugs (Pentatomidae: *Linctus* spp.)	Persistent, circulative
Fungi		
Yeast spot of bean, coffee, etc.	Hemipteran fruit or seed feeders	Noncirculative but persistent
Dutch elm fungus	Bark beetles	Persistent, carried externally by adults
Nematodes		
Pine wilt nematode	Long-horned beetles	Persistent, nematodes infest spiracles of adults

varieties against diseases now lacking satisfactory sources of resistance.

ARTICLE OF FURTHER INTEREST

Bacterial Survival and Dissemination in Insects, p. 105–107.

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