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Insects and the Plant Viruses

L. D. Christenson, Floyd F. Smith

The Russian scientist D. Iwanowski demonstrated in 1892 that sap from tobacco plants with a mosaic disease is infectious after passing through a bacteria-proof filter. It was the first discovery of an amazing group of agents that cannot be seen with ordinary microscopes and that now are called viruses. Many of our most serious and difficult plant-disease problems have been shown to be the results of infections of plants by these minute entities, which are smaller than bacteria. A few of the many different kinds of viruses are even smaller than the largest molecules known to chemists.

Tulip mosaic, peach yellows, aster yellows, sugar-beet curly top, phloem necrosis of elm, tobacco mosaic, raspberry mosaic, blueberry stunt disease, potato leaf roll, pea mosaic, tomato spotted wilt, and sugarcane mosaic are examples of plant diseases caused by viruses. Virus agents also cause serious diseases of man and animals—smallpox, measles, mumps, the common cold, rabies, distemper, and foot-and-mouth disease. Others, like the sacbrood virus of honey bees, infect invertebrate animals.

For a long time we knew little about the nature of viruses. Now, as a result of the studies of W. M. Stanley, F. C. Bawden, N. W. Pirie, and others, they are believed to consist of complex nucleoproteins that have some of the attributes of living organisms. Like living organisms, the individual virus particles can reproduce or multiply. They also can change or mutate during the multiplication process. They do not seem able to grow or multiply, however, except within the living cells of their hosts, and, unlike living organisms, they cannot carry on the complicated processes of respiration, digestion, and other metabolic functions.

Most of the plant viruses have been discovered since 1900, but they are not of recent origin. Old Dutch masters recorded in their paintings the variegations in the petals of tulips caused by a virus now known as tulip mosaic. Dutch bulb growers knew as early as 1637 how to graft healthy bulbs with variegated bulbs to get the coveted many-colored flowers even though they did not know what caused them. Potato viruses had become so abundant in Europe by 1775 that the production of potatoes had to be abandoned in many areas because of what was then termed the "running-out" of potatoes. In the United States, the virus disease now known as peach yellows was described as early as 1791. We have evidence that it was doing damage in peach orchards as early as 1750.

Only a few viruses kill the plants they infect. Plants affected by most of them never recover, but they do not die as a result of the infection. Their growth and productivity may be seriously affected. Some species and varieties of plants apparently are not attacked by viruses. Others may be tolerant of them or only mildly affected when their tissues are invaded by the virus particles. Trees, shrubs, other plants in uncultivated areas, and weeds on farms may be infected by viruses that also attack cultivated plants. When that is so, the wild plants serve as important sources of danger to the cultivated plants. Otherwise the viruses in the uncultivated plants are not economically important. No viruses are yet known that attack coniferous trees, such as pine and spruce.

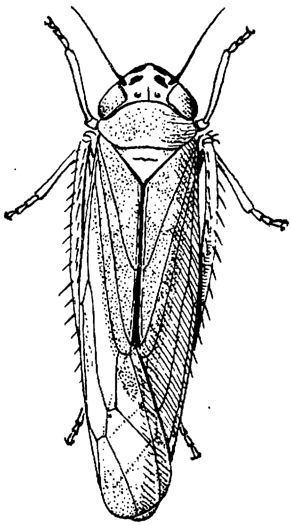
Our cultivated crops annually suffer heavy losses because of virus diseases. Phony peach has plagued peach growers in the Southeastern States for at least half a century, making it necessary for them to take out more than 2,600,000 peach trees. Years ago in the Northeastern States, peach yellows destroyed the productiveness of hundreds of thousands of trees. Sometimes it was necessary to destroy entire orchards. Tobacco mosaic has been estimated to cause an annual loss of millions of pounds of tobacco. Viruses have seriously affected the production of potatoes each year. To reduce their losses, the growers here and in England and other countries have to expend large sums to get healthy seed potatoes grown in areas where potato viruses are not serious. Production of head lettuce in the East has not been profitable because of infection by the virus known as aster yellows. Losses caused by the curly-top virus in sugar beets have been so severe in the Western States that some sugar factories have had to be abandoned. The same virus has caused crop failures in tomato fields. Similar heavy tolls may be levied by the viruses that attack many of our ornamental plants and flowers.

Plant diseases caused by viruses spread in several ways. Some are so infectious that contact between the leaves of normal and diseased plants is all that is necessary. Highly contagious diseases such as these may be spread by mechanical means. A few instances of spread through seeds are known. A serious method of spread is through the use of parts of infected plants to start new plantings. For example, viruses that persist from year to year in potato tubers, in bulbs, and in rhizomes infect plants growing from them. Viruses may also be spread through cuttings or suckers from infected plants and through budding and grafting procedures employed in nurseries.

Insects are the worst spreaders. A Japanese scientist in 1901 found that a leafhopper could transmit stunt disease of rice from diseased rice plants to healthy plants.

The first insect to gain prominence in North America as a carrier of a plant virus was the beet leafhopper. It was found to be spreading curly-top disease in sugar-beet fields in Utah and other Western States only a few years after the discovery of the insect carrier of stunt disease of rice. We now know that many of our plant virus disease outbreaks are the result of insect-carrier activity, and it is suspected that insects are involved in the spread of many other plant virus diseases.

Insect carriers of plant viruses are known to occur in only six of the major orders of insects—the Homoptera (aphids, leafhoppers, whiteflies, mealybugs, scales), Thysanoptera (thrips), Heteroptera (plant bugs, lace bugs), Coleoptera (the beetles), Orthoptera (grasshoppers), and Dermaptera (earwigs). Most of the carriers have sucking mouth parts, and among them the aphids and leafhoppers seem to be the most proficient. A few insects with chewing mouth parts, such as grasshoppers and leaf-feeding beetles, also spread certain virus diseases.



Six-spotted leafhopper.

To accomplish transmission, the vector has to get the virus from a diseased plant, which it does while feeding, and then move to a healthy plant, which it infects during the feeding process. With the sucking insects, the virus particles apparently are injected into plants with the saliva.

The relationships between plant viruses and their vectors have commanded the attention of many entomologists, plant pathologists, and other biologists. Striking advances have been made, and we now know a great deal about many insects that transmit viruses, something about what happens to the virus during its period in the insect body, and something about the factors involved in the transmission process. There is still much to be explained, however: We do not know why certain species can transmit viruses while other similar insects cannot, or why certain insects can transmit so many different kinds of plant viruses but not others. The many other vectors awaiting discovery also remain a challenge.

PLANT VIRUSES are considered as belonging to two general groups.

In the group called the nonpersistent viruses, the insect carrier can transmit the virus soon after feeding on a diseased plant. This ability to cause new infections is quickly lost, however, after the insects feed on healthy or immune plants. A starvation period before feeding on infected plants usually increases the transmission efficiency of the vectors of the viruses, which usually can be transmitted by mechanical means, as by wiping the sap of an infected plant over the leaves of a healthy plant. The insect carriers sometimes include many different kinds of insects. Many viruses transmitted by aphids and chewing insects belong to this group. Perhaps some of the nonpersistent viruses are transmitted through contamination of the mouth parts of the insect carriers with virus particles, but for many others the transmission process does not seem to be that simple.

The other group includes the persistent viruses. When they are taken in with the food of their vectors, an interval (the incubation, or latent, period) is necessary before the insects can infect healthy plants with them. Once having the ability, insect carriers of persistent viruses usually can transmit them to healthy plants for an extended period, often for life. In two instances involving leafhoppers, persistent viruses are transmitted to the succeeding generation through the eggs. Some of these viruses are transmitted by only one or a few closely related insects. Most of the viruses that leafhoppers transmit are persistent viruses. A few aphids or other insects also transmit persistent viruses.

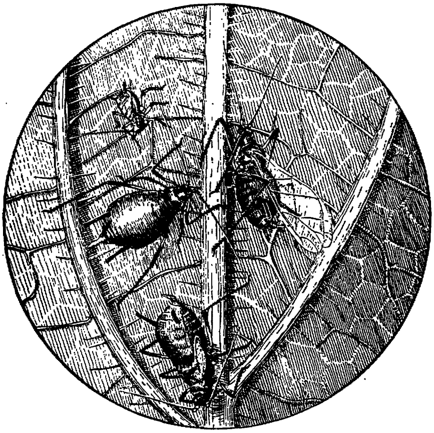
The incubation period of the persistent viruses in insects sometimes lasts only a few hours or less. It may last as long as 5 days in some aphids or several weeks in some leafhoppers. The incubation period of the virus that causes western X-disease of peach is usually longer than 30 days in the geminate leafhopper. Incubation periods as long as 40 days have been reported for some leafhoppers that transmit aster yellows, although in most of them the period is about 2 weeks. One of the four leafhopper carriers of phony peach in the Southeastern States has transmitted the disease to healthy peach trees 14 days after first feeding on a phony tree, but in another leafhopper the shortest incubation period observed thus far has been 19 days. Temperature may influence the length of an incubation period of a virus in an insect.

The meaning of the incubation period of the viruses is moot. Some investigators believe it is a true incubation period, during which the virus goes through some kind of necessary developmental or reproductive stage. Others consider it merely the time necessary for the virus particles to make their way through the intestinal walls of the insect into the blood stream and thence into the salivary glands, where they can be introduced with saliva into healthy plants during feeding.

Both points of view can be justified, depending on the virus involved. Some leafhoppers transmit persistent viruses throughout their lives once they become infective. Others may lose the ability after a period. In some individuals the ability to transmit a virus may become much less pronounced as they near the end of their life span—perhaps the original supplies of virus taken in have become exhausted during the intervening feeding periods on healthy plants and there has been no multiplication of the virus particles within the insect, or at least not sufficient reproduction to maintain an infective charge of the virus. There is no evidence that viruses undergo biological changes in insects, but one scientist has reported that clover clubleaf virus reproduces in its leafhopper carriers. The leafhoppers remain infective through successive generations long after there would be any chance for the original quantity of virus to be involved. There also seems to be convincing proof that the virus causing aster yellows and the one that causes stunt disease of rice in the Orient multiply in their insect carriers.

Some insects that transmit viruses can become infective after a feeding period of only 1 minute or after only a single feeding on a diseased plant. Different species vary with respect to their efficiency in transmitting virus diseases, and there are instances where the nymphs or immature stages seem to be less efficient than the adult insects. Some vectors can pick up viruses while they are in immature stages but cannot transmit them until the adult stage is reached. The suggested explanation, in the case of a leafhopper carrier of aster yellows, is that the incubation period is not completed before the nymphs reach the adult stage. But that is not the explanation in the case of thrips, which transmit spotted wilt virus, because adults become infective only after picking up the virus while in the larval stage.

A plant virus may have a single species of insect serving as its vector, or there may be several kinds able to transmit the same virus. Sometimes the latter are entirely unrelated species. Single insects can infect plants with virus diseases, but even an infective individual cannot cause an infection every time it feeds on a healthy plant. In some instances this seems to be be-



Macrosiphum ambrosiae, aphids.

cause the virus must be introduced into certain types of plant tissue which the vector does not always reach with its mouth parts; in other cases the reasons are not apparent. Viruses do not seem to affect their insect carriers in any way, even though they cause serious diseases of plants.

THE APHIDS, or plant-lice, have developed the ability to serve as carriers of plant viruses to the greatest degree. These minute, soft-bodied insects feed by sucking sap through their beaks, which they insert into plant tissues. They attack practically all kinds of plants. Most species produce both winged and wingless individuals. The former are chiefly responsible for the spread of virus diseases in fields.

The green peach aphid is outstanding among aphid carriers of plant virus diseases. It is known to transmit more than 50 kinds, mostly of the nonpersistent type.

The green peach aphid occurs almost everywhere and feeds on many kinds of plants. It is a serious pest of potatoes because it can transmit leaf roll and other viruses. In potato-growing areas where the winters are mild, the green peach aphid spends the winter on weeds and such vegetables as spinach and kale. Winged individuals produced on the winter host plants migrate into the potato fields when the plants are small. As they move from plant to plant, the winged migrants leave a few young aphids here and there and spread potato viruses from diseased plants to healthy plants. The young aphids left behind start new aphid colonies throughout the potato field. When the colonies become overcrowded, enormous numbers of winged aphids may be produced. They swarm over the field and cause another wave of infection. Individual potato farmers are helpless in their efforts to protect their crops when tremendous numbers of migrating aphids are present.

In northern Maine and other potato-growing areas where winters are cold, the green peach aphid overwinters in the egg stage. The eggs are laid on twigs of peach and plum trees by female aphids, which are produced in the late summer or early fall. Relatively few winged aphids are produced in colonies developing from these eggs, and consequently infestations in potato fields are extremely light early in the spring. Although large numbers of winged aphids may be present later in the summer, there is usually not so much spread of virus diseases in northern potato-growing areas as there is in areas with warmer winters. The amount of potato leaf roll in the following year's crop may be predicted rather accurately from the abundance of the winged forms of peach aphid during the summer.

The green peach aphid and other aphids that develop on potatoes and other plants may migrate across a gladiolus field and pick up yellow bean mosaic virus. The virus causes only mild symptoms in gladiolus, but when the aphids transmit it to beans, a destructive disease results. Celery in Florida is infected with cucumber mosaic by aphids which pick it up as they feed on commelina, a weed that grows along ditchbanks.

Lilies in fields containing a few plants infected with the nonpersistent coarse mottle and cucumber mosaic vi-

Examples of Plant Viruses and Some of Their Insect Vectors

Virus	*Vector*	*Common name*
Potato spindle tuber	*Melanoplus* spp	grasshoppers.
	Epitrix cucumeris	potato flea beetle.
	Systena taeniata	flea beetle.
	Disonycha triangularis	leaf beetle.
	Leptinotarsa decemlineata	Colorado potato beetle.
	Lygus oblineatus	tarnished plant bug.
	Myzus persicae	green peach aphid.
Strawberry yellow edge	*Pentatrichopus fragariae*	aphid.
Strawberry crinkle	*Pentatrichopus fragariae*	aphid.
Onion yellow dwarf	*Aphis gossypii*	melon aphid.
	Myzus persicae	green peach aphid.
	Brevicoryne brassicae	cabbage aphid.
	Aphis maidis	corn leaf aphid.
	Other Aphidae	At least 50 species of aphids transmit this virus.
Cucumber mosaic	*Aphis gossypii*	melon aphid.
	Myzus persicae	green peach aphid.
	Myzus circumflexus	crescent-marked lily aphid.
	Myzus solani	foxglove aphid.
Raspberry mosaics	*Amphorophora rubi*	aphid.
	Amphorophora sensoriata	aphid.
Pea mosaic	*Macrosiphum pisi*	pea aphid.
	Myzus persicae	green peach aphid.
Potato leaf roll	*Myzus persicae*	green peach aphid.
	Myzus circumflexus	crescent-marked lily aphid.
	Myzus solani	foxglove aphid.
	Macrosiphum solanifolii	potato aphid.
Sugarcane mosaic	*Aphis maidis*	corn leaf aphid.
	Hysteroneura setariae	rusty plum aphid.
Citrus quick decline	*Aphis gossypii*	melon aphid.
Potato yellow dwarf	*Aceratagallia sanguinolenta*	clover leafhopper.
	Aceratagallia curvata	leafhopper.
	Aceratagallia longula	leafhopper.
	Aceratagallia obscura	leafhopper.
Sugar-beet curly top	*Circulifer tenellus*	beet leafhopper.
Pierce's disease of grapevines	*Draeculacephala minerva*	leafhopper.
	Helochara delta	leafhopper.
	Carneocephala fulgida	leafhopper.
	Other Cicadellidae	At least 14 species can transmit this virus.
	Aphrophora annulata	spittlebug.
	Aphrophora permutata	spittlebug.
	Clastoptera brunnea	spittlebug.
	Philaenus leucophthalmus	meadow spittlebug.
Phloem necrosis of elm	*Scaphoideus luteolus*	leafhopper.
Peach yellows	*Macropsis trimaculata*	plum leafhopper.
Phony peach	*Homalodisca triquetra*	leafhopper.
	Oncometopia undata	leafhopper.
	Graphocephala versuta	leafhopper.
	Cuerna costalis	leafhopper.
Western X-disease of peach	*Colladonus geminatus*	geminate leafhopper.
Papaya bunchy-top	*Empoasca papayae*	leafhopper.
Cranberry false-blossom	*Scleroracus vaccinii*	blunt-nosed cranberry leafhopper.
Blueberry stunt disease	*Scaphytopius* sp	leafhopper.
Tomato spotted wilt	*Thysanoptera*	thrips.
Tobacco mosaic	Aphidae	A few aphids have been reported to transmit this virus.
	Melanoplus differentialis	differential grasshopper.
Latent potato virus (potato virus X).	*Melanoplus differentialis*	differential grasshopper.
Tobacco ringspot	*Melanoplus differentialis*	differential grasshopper.
Cotton leaf curl (in Africa)	*Bemisia gossypiperda*	whitefly.

ruses soon become almost completely diseased when the fields are planted near potatoes or other plants where the aphid carriers of these diseases develop. Lily rosette, a persistent virus, is transmitted by the melon aphid after an incubation period of the virus in the aphid lasting 3 or 4 days. This aphid develops on young lily plants; both the wingless aphids (which crawl to adjacent plants) or winged migrants (which fly to plants farther away) may spread lily rosette.

The melon aphid also transmits a virus that causes a condition known as lily symptomless disease. The disease has spread slowly throughout most commercial stocks of lilies. In itself it is not serious, but when the same plants get cucumber mosaic the double infection termed necrotic fleck makes them worthless. Necrotic fleck was chiefly responsible for the failure of Easter lily bulb production in the United States. To meet our needs, as many as 25 million Easter lily bulbs have been imported in a year.

The strawberry aphid in England transmits three viruses of strawberries, which cause the "running out" of desirable varieties. This aphid and two related species occur in the United States and live throughout the year on strawberry plants. Similar diseases and possibly others are devastating strawberries in the United States. These three strawberry aphids have been shown to be vectors of strawberry viruses in America and are believed to be chiefly responsible for their dispersal under field conditions. The Department of Agriculture has helped the strawberry industry by locating virus-free strawberry plants of the more valuable varieties and furnishing foundation stocks to cooperating nurseries for mass propagation and replacement of infected plants.

Winged aphids from overwintering pea aphid colonies on alfalfa transmit a serious virus disease of peas, which kills the tips and interferes with the productivity of the plants.

Aphids may also spread viruses that affect trees. An example is the citrus quick decline disease, which in a few years has caused the loss of many thousands of orange trees in California. The vector of quick decline is the melon aphid. Another aphid, which does not occur in the United States, is the vector of a similar virus disease of citrus in South America.

THE LEAFHOPPERS are our second most important carriers of plant viruses. They are small, slender, variously colored insects, which have sucking beaks similar to those of the aphids. They are active jumpers. The adults fly freely and some of them can cover long distances in migratory flights. A characteristic habit of young and adults is that of walking sideways. All leafhoppers are plant feeders. Certain kinds are called sharpshooters, and other names such as whitefly and greenfly have been used for some of them.

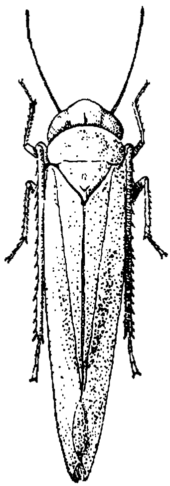
Leafhoppers transmit at least three serious virus diseases to peach trees. The oldest is peach yellows. Its vector was a mystery until the 1930's, when it was discovered that the plum leafhopper is the carrier.

The plum leafhopper feeds on the twigs and is seldom seen on the leaves. Plum is its favored host. Rarely is it found on peach. The leafhopper may obtain the virus, which it transmits to peach trees, from peach and plum trees. The latter are symptomless carriers of the yellows virus. In orchards adjacent to woodlands, correlations between the numbers of the leafhoppers, the abundance of wild plum, and the amount of yellows disease in peach have been noted. No other vectors of peach yellows have been discovered.

The plum leafhopper is present in all areas where peach yellows occurs. Although peach yellows is no longer a serious problem, new cases each year give warning that the vector is still active and that peach growers in the Northeastern States cannot afford to relax their vigilance with respect to the disease.

Phony peach disease poses a problem

for peach growers in Southeastern States, particularly in parts of Georgia and Alabama, where it is difficult to control with the usual method of inspecting orchards and removing all diseased trees. An intensive 12-year search for vectors ended in 1949, when it was



Leafhopper.

announced that four leafhoppers can spread the disease. They are all general feeders.

Two are believed to be main vectors in spreading the disease in orchards. They spend the winter as adults and occasionally as nymphs under trash and debris in woodlands and possibly along ditchbanks. In spring they become active, leave the woods, and move to a variety of plants, including peach trees, where they feed on the twigs. When preferred herbaceous plants later become available, they leave the peach trees and go to them. Very few are found on peach trees in summer but they reappear on this host early in the fall. They continue to feed on the twigs of peach trees even after the trees become fully dormant until they are forced into hibernation by cold weather.

Presumably phony peach spreads mostly during the periods in spring and fall when the leafhoppers are on peach trees. After sucking sap from infected trees, they cannot cause phony infections until after an incubation period of 14 to 40 days. Infective leafhoppers can transmit the phony peach virus for a long time, possibly for life, but we do not know whether the virus persists in them through the long periods of hibernation. When feeding, the hoppers insert their beaks into the woody tissue of peach twigs where the phony peach virus seems to be localized. They can obtain the virus from both diseased peach and wild plum trees, but not all peach trees seem to be equally good sources of the virus.

Fruit growers in the Pacific Northwest are plagued by several devastating peach and cherry virus diseases. One, the western X-disease of peach, is transmitted by the geminate leafhopper, which might also spread a little-cherry condition caused by the same virus. The incubation period of the virus in this leafhopper is usually longer than 30 days. Single leafhoppers have transmitted western X-disease; some have retained the ability to cause infections for at least 80 days. The leafhopper prefers legumes and grasses, but it feeds on many other plants. Nymphs seldom occur on peach trees but the adults frequently visit them and other stone fruits. The leafhopper also occurs on chokecherry, a wild host of the western X-disease.

At least 14 species of leafhoppers transmit the virus that causes Pierce's disease of grapevines. The same virus also infects alfalfa, causing a disease called alfalfa dwarf. A remarkable thing about the leafhopper carriers of Pierce's disease is that they are all closely related and belong to the same subfamily, which includes all known vectors of phony peach disease. The leafhoppers vary greatly in their efficiency and importance as vectors of Pierce's disease. Infective leafhoppers have been found far from vineyards or alfalfa fields—perhaps there are still other plant hosts of the virus.

Aster yellows virus affects many vegetables, flowers, and other herbaceous plants. In the Eastern States only one strain of the virus and only one vector, the six-spotted leafhopper, are known. A number of leafhoppers can transmit the western strains of the virus. The strain affecting celery, for example, is carried by at least 22 kinds of leafhoppers. The geminate and mountain leafhoppers transmit the celery strain of the virus, but they cannot transmit a related strain that causes yellows disease in asters. Both of these western virus strains, however, are transmitted by the six-spotted leafhopper. This curious relationship, and a similar situation found among the leafhoppers which transmit potato yellow dwarf virus, suggest that some virus strains may have developed in relation to their insect vectors rather than their plant hosts. The vector of aster yellows in the East cannot cause infections when exposed to high temperatures, but it regains the ability when the temperature goes down.

The wide variety of leafhoppers that transmit aster yellows, Pierce's disease of grapevines, and phony peach has brought up the point that the ability to transmit virus diseases may be determined somewhat by the ability and inclination of leafhoppers to feed on a definite part of the plant host. Of course that would be true only of the species that meet all biological requirements necessary for them to serve as vectors.

Curly-top virus causes serious diseases of sugar beets, tomatoes, and beans in Western States. The only vector known in this country is the beet leafhopper, apparently an introduced species with no close relatives in the New World. The curly-top problem and its leafhopper vector are the subjects of another article, on page 544.

Other kinds of sucking insects spread plant virus diseases. Besides many leafhoppers, four species of froghoppers, or spittlebugs, transmit Pierce's disease of grapevines. A lace bug is a vector of a virus disease of sugar beets. Mealybugs and whiteflies transmit serious diseases of cacao, cassava, or cotton in other countries. A scale insect may be involved in the spread of sudden death of clove trees.

THRIPS are tiny insects that feed by macerating the surface layers of plant cells and then sucking up the juices. Certain thrips are notorious as vectors of the spotted wilt virus of tomatoes and pineapples. The virus, or strains of it, occurs in many parts of the world and affects many kinds of plants. It causes one of the major diseases of pineapples in the Hawaiian Islands. Adult thrips cannot acquire the virus by feeding on infected plants. However, the adults that develop from nymphs that have fed on diseased plants become infective; the virus survives the pupal, or resting, stage which the insects undergo. In spotted wilt of tomatoes, the incubation period of the virus in the insects is 5 to 7 days and the ability to cause infections is retained for several weeks. Thrips develop on a wide variety of host plants and can cause severe damage even when not transmitting viruses.

Insects with biting and chewing mouth parts are involved in the transmission of a few plant viruses. Grasshoppers and leaf-feeding beetles are vectors of the highly infectious disease of potatoes called spindle tuber. Cucumber beetles transmit a mosaic disease of cucumber. The role of these insects—of spindle tuber at least—seems to be that of a mechanical carrier. The disease is also spread by many kinds of insects.

The differential grasshopper apparently can transmit tobacco mosaic, latent potato virus, and tobacco ringspot virus to healthy tobacco plants. Aphid vectors had been reported for tobacco mosaic, but repeated trials have failed to implicate insects in the transmission of latent potato virus or tobacco ringspot virus. The differential grasshopper apparently can infect tobacco plants immediately after feeding on diseased plants; infection results after only one or two feedings on a healthy plant. The transmission process is believed to be a simple mechanical transfer of virus particles on the mouth parts of the grasshopper. It is likely that virus particles on the feet of the grasshoppers may also start infections.

SOME OF THE REPORTS of insect transmission of plant viruses upon further investigation may be found to be a result of direct-feeding injuries that resemble symptoms of virus diseases. The foxglove aphid on lilies and several vegetable crops and an aphid on carnation cause spotting and distortion of leaves that look like viruses in the same hosts. Tarnished plant bugs cause stunting, distortion, and dead areas much like virus infection in some plants. Alfalfa yellows and a condition in potatoes known as hopperburn were suspected of being virus diseases until investigations showed that they resulted from direct feeding by the potato leafhopper. Feeding by the broad mite causes mottling, distortion, and stunting that have been mistaken for virus diseases. Infections by leaf-infesting nematodes result in yellowing, mottling, and dead areas like virus symptoms. Such direct injuries appear to be due to toxic principles in the saliva injected while feeding or to mutilation of cells in very young tissue that later develops abnormally or declines prematurely. Symptoms left by the potato leafhopper result from injury to vascular tissue in the plants, which interferes with translocation of food.

IN A FEW DISEASES, the viruses move into new shoots less rapidly than growth occurs. When that happens (for example, when dahlia roots are infected with spotted wilt) healthy plants can be obtained from shoots that grow from the crowns if cuttings are removed before they are invaded by the virus. The use of healthy planting material is an obvious first precaution for reducing losses caused by many virus diseases.

Rotation of crops sometimes eliminates virus sources in volunteer plants that would infect the crop if it were grown in the same field the following year.

Rogueing, the removal of infected plants as soon as symptoms of diseases appear, maintains or even improves the health of potato, raspberry, strawberry, and other crops. The procedure, together with nursery practices to make sure that young trees used for new plantings are not infected, has been the principal method for controlling serious virus diseases of stone fruits such as peach yellows, phony peach, and peach mosaic. In isolated areas, where the vectors apparently are not very active, it has even been possible to achieve eradication of these diseases by this method.

When they are available, the use of resistant or immune varieties is an effective way to prevent losses caused by virus diseases. Losses can also be avoided by growing crops in areas where serious virus diseases are not present or where vector activity is at a low ebb.

Means have been sought for curing plants affected by virus diseases with heat treatments or chemicals administered internally. Often viruses may be killed by exposures to high temperatures that are tolerated by the infected plant tissue. Heat cures are of practical value for eliminating the viruses of sereh and chlorotic streak diseases in sugarcane seed pieces. For stone fruits a heat treatment has been suggested for yellows and X-diseases of peach but has not been used practically as yet. Its value is primarily in providing disease-free planting material.

A practical chemical treatment for inactivating viruses in plants, usable under field conditions, would be a boon to agriculturists everywhere.

The spread of plant viruses may also be prevented or retarded by methods that eliminate or reduce the insect carriers below critical transmission levels. The problem is not simple. Treatments must be exceptionally effective, even more than when the direct injury caused by the insects is the only concern. A light population of the insect carriers may be able to infect many additional plants when abundant sources of virus are available, or start a new outbreak of disease. The presence of numerous widely distributed carriers with different seasonal histories further complicates the problem. Because insects may move in constantly from untreated areas, some of them already infective, continuous protection throughout the growing season may be required when insecticides are used. Despite such difficulties, some progress can be reported.

Some benefits have been obtained with methods for reducing the numbers of insect carriers or for preventing or avoiding their activity without using insecticides. The elimination of host plants of insect carriers is often beneficial. Cloth of a special coarse weave, supported by posts and wire, effectively excludes the leafhoppers that transmit yellows infection to China asters.

Potato virus diseases are largely controlled by using seed potatoes grown in isolated areas or in places where the aphid vectors are scarce. Relatively few potatoes are infected under those conditions, and the seed pieces produce a high proportion of healthy plants. Northern locations or high altitudes with cool temperatures and almost constant winds are best for growing seed potatoes, because those conditions are unfavorable for aphid development or flight. Frequent rogueing and applications of insecticides help to maintain the healthy seed stock. Similar procedures are used for developing and maintaining healthy source stocks of strawberries in England, and they may be practical for lilies, gladiolus, and other economic plants in the United States.

Many experiments have been made to determine the usefulness of insecticides in controlling the carriers of plant virus diseases. The materials available before 1940 were seldom effective enough. The situation has improved with the development of new insecticides, such as DDT.

Applications of insecticides to cultivated crops can be expected to control virus diseases best if the diseases are spread solely within the crop by the insect carriers that develop on the crop. Residual insecticides may be of value in reducing the amount of disease caused by carriers coming in from outside sources. To be effective, the insecticide must kill rapidly enough to destroy the insects before they can do much feeding. They must also remain toxic to later invaders for several days or until the next application of insecticide is made. The application of insecticides to vector breeding areas to destroy the insects before they reach cultivated plantings may have merit in certain situations.

DDT has been the most useful of the new insecticides for controlling insect carriers of plant virus diseases. It is effective against nearly all leafhoppers and it destroys some of the important aphid vectors. It is now almost universally applied to potato fields to eliminate aphids. The applications greatly reduce the number of wingless aphids and winged summer migrants which develop, and the spread of potato leaf roll is now much less than in former years. Aster yellows has been reduced by about 90 percent in lettuce fields in New York and Maryland by DDT applications, which destroy the six-spotted leafhopper, the most important carrier of the disease. The DDT residues are also effective against additional leafhoppers that move into lettuce fields each day. Good results with DDT for controlling aster yellows in carrots have also been reported.

DDT has been studied in Western States to determine its usefulness in preventing curly-top virus infections in sugar beets, tomatoes, and beans. The DDT reduces the number of beet leafhoppers and has good residual toxicity, but it does not prevent the feeding of the leafhoppers that reinfest the fields. The incidence of the disease in tomatoes therefore may not be appreciably reduced by DDT if reinfestation occurs. In fields where reinfestation does

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not occur, single applications may give good results. Insecticidal control of leafhoppers on weed hosts growing on idle and waste land, which contribute large populations to cultivated areas, has been used in California to combat a serious curly-top problem. Experiments with the method have also been made in Idaho. When control of the leafhoppers in their breeding grounds is undertaken, it is desirable to eliminate the host plants of the insects as fast as possible, and replace them with plants, such as grasses, on which the beet leafhoppers do not breed.

First results of experiments suggest that DDT may have an appreciable effect on the insect carriers of phony peach disease and that it may be possible to retard its spread with DDT, but much remains to be done on the problem before practical suggestions for the use of DDT for the purpose can be made.

Systemic insecticides, which invade entire plants after being taken in through the roots or leaves, are toxic to aphids that feed on the treated plants. The spread of yellows in beets and other virus diseases in strawberries, all aphid-transmitted, is said to have been greatly reduced through the use of systemic insecticides on farms in England. Studies in the United States indicate that the method has possibilities for aphid-transmitted viruses, which attack ornamental plants, such as lilies, tulips, narcissus, and other plants propagated in nurseries. The method may also be feasible for treating food crops if it is found that the insecticide or its decomposition products in the plant are not harmful.

In greenhouses, the spread of viruses is easily prevented by maintaining strict control over all insects. Fumigation with various materials or the use of aerosols containing one of the new organic phosphate insecticides are effective.

The new advances in insecticidal control of plant virus diseases probably will lead to others. With such an array of new insecticides for evaluation and with the new equipment for applying them rapidly and effectively, the entomologists may make even greater contributions to the control of plant virus diseases than has been possible in the past.

But it is too much to expect that the problem will be solved entirely even then: Still needed will be cooperation among growers in control programs, constant emphasis on preventive measures, and the enforcement of quarantines to prevent the spread of viruses into new localities and to prevent the introduction of additional virus diseases into the United States.

L. D. CHRISTENSON *is entomologist in charge, oriental fruit fly investigations, Bureau of Entomology and Plant Quarantine, in Hawaii. He attended the Utah State Agricultural College, the University of Minnesota, and the University of California. From 1929 to 1942 his principal assignments were concerned with studies of the relationships of insects to sugarcane, cotton, and stone fruit diseases in Cuba and in Southern and Western States. From 1946 to 1951 he was assistant to the chief of fruit insect investigations, Bureau of Entomology and Plant Quarantine.*

FLOYD F. SMITH, *a senior entomologist in the Bureau of Entomology and Plant Quarantine, has devoted 28 years to the study of insects affecting greenhouse and ornamental plants. He has published many articles on the biology and control of those pests and on insects as vectors of plant diseases. In recognition of his research on the aerosol method of applying insecticides in greenhouses, the Society of American Florists gave him an award for the most important contribution to floriculture in 1947. He is a graduate of Ohio State University.*

Seed-corn maggot.