descriptions of plant pathogenic bacteria, their reactions on culture media, symptoms of the diseases they produce, their host plants, geographical distribution, control methods if known, and citations to research literature.

How does a plant pathologist make sure that a plant disease is caused by a given species of bacterium? Robert Koch in 1882 worked out the rules of proof to follow for animal diseases. The rigid logic of his requirements applies equally well to bacteria causing plant disease.

Briefly stated, the postulates of Koch require that: (1) The bacterium must be associated in every case with the disease, and conversely the disease must not appear without it. (2) The micro-organism must be isolated in pure culture and its specific morphological and physiological characteristics determined. (3) When the host is inoculated with the bacterium under favorable conditions, the characteristic symptoms of the disease must develop. (4) The micro-organism must be reisolated from the inoculated plant and identified as that first isolated from the diseased host.

In this brief review we have not attempted to present detailed information on individual diseases. Losses caused by various important bacterial diseases, symptoms, means of spread and control measures when known are given in other articles on specific crops.

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Viruses, a Scourge of Mankind

C. W. Bennett

Few kinds of living organisms are immune to viruses. Man, domesticated and wild animals, insects, plants, and even bacteria succumb to their attack. They have been a scourge of mankind since before the dawn of recorded history. Smallpox, for example, existed in China in 1700 B. C. Measles, mumps, influenza, and scarlet fever are other virus diseases that plague humans.

The virus diseases of plants also probably have existed for many centuries. Their importance on crop plants has increased tremendously in the past 50 years—since 1900 more than 200 new plant viruses have been discovered. Many of them have done widespread damage to crop plants.

Curly top caused almost complete abandonment of the sugar beet industry in parts of western United States from 1916 to 1932 and still causes severe injury to tomatoes, beans, and a number of other crops. Sugarcane mosaic caused extensive losses to the sugarcane industry in the United States, Argentina, Brazil, and other countries beginning about 1917. Spotted wilt has become widespread and now causes losses to tomato and other crops in many parts of the world. Since 1940, swollen shoot has caused extensive damage to the cacao industry of west Africa. Virus diseases of citrus have become more destructive and from 1936 to 1946 tristeza caused the loss of 7 million orange trees in the state of São Paulo, Brazil, alone. It has attacked or now threatens other millions of trees in various tropical and subtropical areas.

This increase in destructiveness of virus diseases and in the number of known viruses has come about largely as a result of the expansion of agricultural enterprises and the increased movement of plants and plant products in recent years.

Disease-producing agents—particularly viruses—apparently have originated in local areas all over the world. Probably through long association have native plants developed a tolerance to the local viruses that enables infected individuals to survive with little injury and often with but little evidence of being carriers of viruses.

When crop plants are introduced into areas where they have not been grown before, they frequently become subject to infection with the native viruses, against which they have had no opportunity to develop resistance. Such a virus may cause extensive losses to a crop plant, not only in the areas of original distribution of the virus, but also in the other areas to which it may spread on the recently attacked crop plant.

The appearance of the yellow wilt virus on sugar beet in the Rio Negro Valley of Argentina when attempts were made to develop a sugar beet industry there in 1929 probably is a typical example of the transfer of a virus from wild plants to a new crop plant. From the beginning of the attempt to establish the sugar beet industry there, the sugar beets were attacked by a virus disease, previously unknown on sugar beet or on any other plant. It caused a yellowing, wilting, and death of all infected plants. Injury was so severe that attempts to grow sugar beets were abandoned about 10 years later after considerable loss to growers and processors. This disease appears still to be limited to South America, but it continues to constitute a potential threat to sugar beets elsewhere.

Many plant viruses have spread over extensive areas from their points of origin. The movement of the tristeza virus of citrus is an example of the extensive spread of a destructive virus disease. Tristeza virus probably originated in South Africa or in southwestern Asia. For many years, possibly for centuries, it appears to have had a limited distribution but since 1930 it (or a similar malady or maladies) has been reported in Australia, Java, California, Louisiana, Argentina, Uruguay, and Brazil. Apparently the chief method of long-distance spread has been by means of infected budwood or nursery stock moved from infested to noninfested areas. After it was introduced into Brazil and Argentina it was spread rapidly by the oriental citrus aphid, *Aphis citricidus*.

Virus diseases produce a wide range of symptoms and types of injury on plants. Sometimes they kill the plant in a short time, as with spotted wilt and curly top on tomato. More often they cause lesser injuries that result in reduced yields and lower quality of product. With respect to general type of the symptoms produced, most viruses are of two rather clearly defined groups: Those that cause mottling or spotting of leaves and those that cause a yellowing, leaf curling, dwarfing, or excessive branching, but little or no mottling or spotting.

The first group, by far the larger, includes such important viruses as those causing cucumber mosaic, peach mosaic, and the tomato spotted wilt. Mosaic diseases are characterized by the production of chlorotic, or yellowish, areas in the leaves and sometimes in the blossoms and other parts. The chlorotic areas may be more or less circular or they may be irregular. The spots vary in size from very small areas to large blotches. Sometimes the chlorotic areas cover a large share, or even all, of the surface of individual leaves.

Some of the mosaic viruses cause conspicuous mottling, spotting, or striping of petals of flowers of some ornamental plants. Many of the variegated tulips are only virus-infected plants of nonvariegated varieties. The Rembrandt variety is a virus-infected strain of the variety Princess Elizabeth. Variegation, or "breaking," of blossoms due to viruses commonly occurs also in wallflower, stock, gladiolus, and flowering peach.

The attractively variegated leaves of the ornamental shrub *Abutilon striatum* are also the result of a virus infection. In the United States the causal virus apparently has no insect vector and variegated and nonvariegated plants of *A. striatum* grow side by side indefinitely with no spread of the variegated condition to the nonvariegated plants. In Brazil the virus is transmitted by the whitefly, *Bemisia tabaci*, and there healthy plants may soon become variegated.

Other mosaic-type viruses cause circular or irregular necrotic—dying—or chlorotic spots on leaves, stems, and fruits, as in spotted wilt on tomato. Ring spots and oak-leaf patterns are symptoms of other virus diseases.

Some viruses produce all these types of symptoms and others as well under specific conditions or on different host plants.

Diseases of the leaf curl and yellows group are caused by viruses that appear to be associated with the vascular system of the plant and produce symptoms that are characteristic of disturbances in this type of tissue. With the leaf curl diseases, such as raspberry leaf curl, sugar beet curly top, and tobacco leaf curl, growth of veins is retarded and the leaves roll or become crinkled. Leaves are sometimes deeper green than normal. The yellows types, such as aster yellows and sugar beet yellow wilt, cause yellowing, stunting, and various types of leaf deformations. Other diseases, such as strawberry stunt, cause dwarfing of the plant and some leaf rolling and thickening. Still others stimulate the production of clusters of thin, wiry shoots as in witches'-broom of oceanspray, or they cause the production of wiry shoots on stems or on main limbs and trunks if trees are attacked. Viruses of the leaf curl and yellows group seem to persist in their insect vectors for longer periods than do viruses of the mosaic group.

Some viruses produce symptoms only under certain environmental conditions or on certain host plants or host combinations. Red raspberry mosaic causes mottling only on leaves produced at low temperatures. Symptoms usually appear therefore only on leaves formed in early spring or late fall. Curly top virus is present in many plants of tree tobacco, *Nicotiana glauca*, in California, but no symptoms are evident. Tristeza virus produces marked symptoms only on citrus trees of certain top and root combinations. For example, both sweet and sour orange trees grow well even though infected with the tristeza virus. Also, trees of sour orange that are grafted onto sweet orange rootstocks show little evidence of injury. However, if the positions of the two types of orange are reversed in the grafted tree so that the top of the tree is of sweet orange and the rootstock is of sour orange, the tristeza virus causes yellowing and dropping of the leaves, gradual dying back of twigs, production of weak shoots on the main limbs, and eventual death of the tree.

Plants may be infected with two or more viruses at the same time. When a plant with one virus disease is attacked by another, usually symptoms of the second disease are merely superimposed on those produced by the first. Occasionally, however, infection by two viruses results in added symptoms. An example is double-virus streak in tomato caused by infection with both tobacco mosaic virus and potato virus X. Tobacco mosaic virus causes mottling and a certain amount of dwarfing. Potato virus X induces mild mottling. When both viruses are present in the same tomato plant a marked increase in injury occurs with the production of extensive necrosis on leaves and stems not characteristic of either virus alone.

Transmission of virus diseases may be

brought about in a number of different ways. Under experimental conditions, many of the mosaic-type viruses can be transmitted mechanically by rubbing juice from diseased plants over the surface of leaves of healthy plants. The addition of a small amount of an abrasive such as carborundum to the juice frequently increases the amount of infection. This method of transmission is of great value in studies of properties, characteristics, and host range of viruses. The majority of viruses, however, have not been transmitted by juice inoculation.

Transmission of sugar beet curly top virus and cucumber mosaic virus by means of dodder, *Cuscuta subinclusa*, was reported in 1940, and a number of other viruses have been transmitted since by it and other species.

The species of dodder used for virus transmission are members of a group of interesting parasitic seed plants belonging to the same family as morning-glory and sweetpotato. They sometimes cause extensive injury by parasitizing clover, alfalfa, and other plants. They attach themselves to their host plants by a type of natural graft union. Because species of dodder have extensive host ranges, plants widely different botanically may be united by a type of natural graft in which dodder forms a connecting link through which several viruses have been found to pass. Thus dodder provides a medium through which viruses may be transferred from diseased to healthy species that cannot be infected by juice inoculation or by insect vectors.

Under field conditions only a few viruses are disseminated by mechanical transfer. Most natural spread takes place through the use of infected vegetative parts for propagation, through infected seeds, and by insects.

The virus of tobacco mosaic probably is the only plant virus spread extensively and chiefly by mechanical means. It occurs in such high concentrations in infected plants, persists for such long periods in infested plant material, and is so easily spread by contact that extensive transmission in tobacco may occur in operations involving handling plants at planting time and in the cultural operations throughout the growing season. Also, it is spread in greenhouse tomatoes when they are cultivated, pruned, tied to supports, or harvested.

Propagation of plants by vegetative means results in the spread of many virus diseases. Most viruses invade plants so extensively that they occur in all parts of the plant, and many of them undoubtedly invade nearly all of the living cells. When buds or scions from virus-infected plants are used for propagation, the new plants are nearly always infected. Likewise, the tubers, roots, offshoots, or other vegetative parts used for propagation carry all of the viruses present in the parent plant. For this reason transmission by vegetative propagation is important in the dissemination of virus diseases of strawberry, raspberry, potato, tree fruits, and many ornamentals. Most of the viruses of those plants are spread by other agencies as well.

Seed transmission of viruses occurs only in relatively few cases. Seeds, for the most part, have a remarkably effective mechanism that prevents the passage of virus into the young embryo from the mother plant. The nature of this mechanism is imperfectly understood, but its effectiveness may be illustrated by the reaction of sugar beet to curly top virus. The curly top virus is known to spread throughout the plant, and seeds of diseased plants carry high concentrations of virus. Despite this fact, however, the virus does not enter the embryo and the infected seeds always produce virus-free plants.

Even the relatively few viruses known to be seed-borne, such as bean mosaic virus, cucumber mosaic virus, lettuce mosaic virus, peach ring spot virus, and dodder latent mosaic virus, are carried only in a portion of the seeds of diseased plants. In most instances, in fact, only a low percentage of such seeds produce infected plants.

Transmission in seed, however, may be important, particularly with diseases like lettuce mosaic, a few diseased seedlings of which may be the source for extensive spread by insects.

Some of the seed-borne viruses are carried in the pollen. When healthy bean plants are fertilized by pollen from mosaic plants, a certain proportion of seeds from the healthy plants produce diseased seedlings. This, however, appears not to be an important method of virus spread.

Insects are by far the most important agents of transmission. Few viruses could persist for long without them.

PROPERTIES AND CHARACTERISTICS of plant viruses have been subjects of study and speculation for many years. Information has increased with more extensive investigations and with the development of new techniques and instruments.

It was learned more than 50 years ago that viruses are very minute entities capable of passing filters so fine that they retained common forms of bacteria and that viruses apparently do not increase outside of living cells.

Further studies made in plants and with plant juices revealed that viruses vary widely in their reactions to a number of environmental conditions. Many appear to be inactivated almost immediately in juice after it is pressed from diseased plants. This probably accounts in part for the fact that many viruses cannot be transmitted by juice inoculation. Other viruses retain activity in plant juice for different periods. Cucumber mosaic virus remains active for only a few hours, sugar beet mosaic virus for 1 to 2 days, and curly top virus for 2 to 5 days. Tobacco mosaic virus is much more resistant, however, and may retain its activity in juice from diseased tobacco plants for several months.

Some viruses that can be transmitted by the juice cannot be recovered from diseased plants after they are dried. Others retain activity in dried plants longer than in plant juice. Curly top virus was recovered from dry sugar beet plants after 8 years, and tobacco mosaic virus has retained its activity in dried tobacco leaves for more than 50 years.

Peach yellows virus is sensitive to high temperatures and can be inactivated in young peach trees by growing them at a temperature of 95° F. for 3 weeks or by immersing dormant trees in water at 122° for 10 minutes. It is destroyed by summer temperatures that prevail for extended periods in some parts of the United States. Aster yellows virus also is inactivated at relatively low temperatures, and its spread is reported to be more extensive in the spring and fall than during the summer because of inactivation of the virus in the leafhopper vector during periods of high temperatures. Most viruses, however, have thermal inactivation points well above the temperatures required to kill the host plants. Some viruses are very resistant to heat. Sugar beet curly top virus is inactivated between 167° and 176°, and tobacco mosaic virus is not inactivated until the temperature rises to 192°.

As a rule, the viruses resist the action of the common germicides. Usually they are not inactivated by the concentrations of bichloride of mercury, carbolic acid, copper, formaldehyde, and alcohol that kill most bacteria. Curiously enough, tobacco mosaic virus, in other respects one of the most stable of viruses, is easily inactivated with alcohol.

The isolation and purification of the tobacco mosaic virus by Dr. W. M. Stanley in 1932 opened the way for more direct and more comprehensive studies of the nature and characteristics of viruses than had been possible by use of earlier methods. The purification of tobacco mosaic virus was soon followed by purification of other plant viruses, some by chemical means and others by sedimentation in high-speed centrifuges.

Most of the viruses that have been obtained in relatively pure condition have been found to aggregate to form crystals or crystal-like bodies that are readily visible under low magnification. Some are even large enough to be seen with the unaided eye. The crystals differ in size and shape depending on the virus and the conditions under which they are formed. Crystals of tobacco mosaic virus are needle-shaped; those of tobacco necrosis virus lozenge-shaped, and those of tomato bushy stunt virus are dodecahedral.

Even after viruses were purified, the virus particles themselves could not be seen because their sizes are below the limits of resolution of the ordinary microscope. That deficiency was overcome with the perfection of the electron microscope, which utilizes radiations of shorter wavelength than those of light. This microscope permitted particles in the size range of viruses to be photographed. For the first time it was possible to determine what viruses look like in photographs, even if not actually to see them.

The plant viruses that have been photographed by means of the electron microscope, numbering a dozen or more, extend over a considerable range in size and shape. Some are long, straight, or tenuous rods. Some are shorter rods. Others are spherical. Tobacco mosaic virus particles are relatively straight rods about 15 millimicrons in thickness and varying in length up to 300 millimicrons, or more. (One millimicron is one-millionth of a millimeter or about one twenty-five-millionth of an inch.) The potato virus X also has rodlike particles, which vary greatly in length and appear to be more flexible than the tobacco mosaic virus particles. Among the viruses that appear to have spherical particles are alfalfa mosaic virus, with a diameter of about 17 millimicrons; tobacco ring spot virus, with a diameter of about 19 millimicrons; and bushy stunt virus, with a diameter of about 26 millimicrons.

The smallest plant viruses are somewhat smaller than some protein molecules. The largest ones are smaller than the smallest known bacteria. Thus, viruses as a group cover a size range between chemical molecules and bacteria, with some overlapping in the lower size range.

All plant viruses so far isolated are similar in chemical composition and contain two essential constituents, nucleic acid and protein.

Nearly all of the plant viruses that have been studied extensively have been found to be complexes of strains. The strains vary in virulence, kind of disease produced, host range, or other characteristics. Curly top virus and tobacco mosaic virus are made up of innumerable strains. Some of these are weak and cause little injury even on susceptible plants. Others are more virulent and cause severe injury. Some strains of curly top virus attack tobacco and tomato; others do not. Two strains of potato yellow dwarf virus appear to be transmitted by different specific vectors.

It may be assumed that these strains have arisen, one by one, from parent strains during the course of years by a process similar to mutation. The relatively large numbers of strains of some of the more common viruses may indicate that some viruses are less stable than others, under the environmental conditions to which they are subjected, hence mutate more readily. This tendency to mutate gives to viruses a degree of adaptability that may be comparable to that possessed by plants and animals.

Recovery from the more severe phases of virus disease is a rather common phenomenon in plants but is limited usually to partial or complete recovery from obvious symptoms and very rarely extends to loss of the virus by infected plants.

One of the first examples of recovery to be discovered was that of the recovery of tobacco from ring spot. A few days after plants become infected with this virus, marked necrosis is produced on a ring of new leaves, but subsequent growth is normal or nearly normal.

Plants from cuttings of recovered plants remain free of severe symptoms, and the diseased plants may be propagated indefinitely by vegetative means without the reappearance of the severe phase of the disease.

Turkish tobacco recovers to a very high degree from curly top. Tomato plants are killed by curly top if the virus is introduced by means of the beet leafhopper; if it is introduced by means of scions from recovered tobacco, however, they usually show only mild symptoms.

Water pimpernel, *Samolus parviflorus*, also shows a high degree of recovery from most strains of curly top virus. Recovery in sugar beet is much less marked. Plants of susceptible varieties usually show little evidence of improvement after they become diseased.

With some viruses and perhaps with most of them, infection by one strain protects against infection or injury from a second strain of the same virus, but no protection is afforded against infection with a totally different virus. Protection of this type is very marked between strains of the tobacco mosaic virus. Juice from a plant with tobacco mosaic, when rubbed gently over the surface of a leaf of a healthy plant of *Nicotiana sylvestris*, produces many small necrotic lesions, which mark points of separate infections. If the inoculated plant has already been invaded by a strain of tobacco mosaic virus, however, no lesions are produced by reinoculation with a second strain of the same virus.

After recovery from one strain of curly top virus, Turkish tobacco plants are very resistant to injury by other strains of this virus. Also, when tomato plants are inoculated with one strain of the curly top virus by means of scions from recovered tobacco plants, they are very resistant to injury by most other strains. Tomato plants "immunized" in this way have been grown successfully under field conditions where all the nonprotected plants were killed.

In contrast, the plants of *Nicotiana glutinosa* and water pimpernel, although they recover from the severe effects of most strains of the curly top virus, are not protected against injury by strains of the virus more virulent than the one already present. No strain of curly top virus offers appreciable protection against either infection or injury in sugar beet.

Although protection between related strains of some viruses is not always evident or complete, cross-protection tests have been of value in identification and classification of viruses from different sources and host plants.

The cross-protection phenomenon may prove to be of value also in certain phases of control of virus disease, particularly diseases such as swollen shoot of cacao and tristeza of citrus. Where either is present, it is known that all susceptible trees must sooner or later become infected from virus sources that are impossible to eliminate. Since this is true, it may prove worth while first to infect all the young planting stock with a weak and relatively harmless strain of virus in order to protect against later infection by more virulent strains of the same virus.

After a plant is infected with a virus disease nothing, as a rule, can be done to restore its health. Therefore, methods of control are directed almost wholly toward prevention of infection or toward development of disease-resistant varieties.

Many practices and precautions are employed to prevent infection with virus diseases. Control of mosaic on tobacco and tomato is obtained largely by avoiding spread of virus by contact during transplanting and cultural operations. Fortunately, few of the virus diseases are so easily transmitted and ordinary cultural operations can be carried on with most plants without danger of spreading virus diseases by contact.

Destruction of plants that serve as sources of infection is of value in the control of a number of virus diseases. Spring infection of fields of sugar beets with mosaic and virus yellows comes largely from infected beets that survive the winter or from beets that are carried through the winter for seed production. Elimination of such sources of virus usually gives a high degree of control. The spread of X-disease on peach can be prevented by removing all infected chokecherries within 500 feet of peach orchards, and the virus diseases of raspberries can be controlled, in most instances, by destroying all wild and escaped brambles in the immediate vicinity of plantings, provided the plantings themselves are not already infected.

Reducing the population of insect vectors by spraying or by other means has value in the control of some virus diseases. Usually it is not possible, however, to reduce the insect populations sufficiently or soon enough to obtain completely satisfactory results. Some virus diseases can be partly controlled by destruction of the hosts of the insect vectors. Extensive reduction of the weed hosts of the beet leafhopper in the Western States would correspondingly reduce the amount of curly top virus carried from desert plants to cultivated fields. In much of this area, reduction in weed hosts comes about naturally under systems of land management in which annual and perennial grasses and other nonhost plants are allowed to replace the weed hosts of the beet leafhopper. Fall spraying to kill leafhoppers on weeds in uncultivated areas has been resorted to also in the program to control curly top.

Virus-free nursery stock is extremely important in the control of virus diseases of strawberry and raspberry. Natural virus spread often is not extensive enough to cause serious damage during the life of plantings started with virus-free nursery stock. That is true also of some of the virus diseases of tree fruits.

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How Insects Transmit Viruses

L. M. Black

Most viruses that cause plant disease are transmitted by insects, principally those that have sucking mouth parts—aphids, leafhoppers, white flies, mealybugs, and tingids. Leafhoppers and aphids are the most important.

Although many plant viruses are without known insect vectors, it is generally expected that insect carriers will eventually be discovered for most of them. There are exceptions. Tobacco mosaic virus and potato latent virus are two viruses that occur in high concentration in infected plants and are stable enough to be spread readily from one plant to another by almost any means that releases juice from a wound in an infected plant and transfers the juice to a fresh wound in a healthy plant. Tobacco mosaic virus is thus transferred by the hands of men working with tobacco plants even though the wounds may be only microscopic in size. It can also be thus transferred by the mouth parts of grasshoppers. Potato latent virus can be transferred from plant to plant when the wind blows the leaves of diseased plants against healthy ones so as to injure both. The mystery about these two viruses is not their transmission by such methods but why potato latent virus is apparently not transmitted by sucking insects and why tobacco mosaic virus is so poorly transmitted.

A few viruses, such as wheat rosette virus and lettuce big-vein virus, contaminate the soil in which diseased