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SIMILARITIES BETWEEN THE DISEASES OF THE VEGETABLE KINGDOM AND THOSE OF MAN AND ANIMALS¹

DR. L. O. KUNKEL

Member of The Rockefeller Institute, Department of Animal and Plant Pathology, Princeton, New Jersey

IN 1918 when an influenza epidemic was raging throughout the • eastern United States, the federal government conducted a survey in certain mining districts of the state of Pennsylvania to determine the distribution of the potato wart disease which had shortly previous to that year been introduced into the United States. Those making the survey encountered some difficulty because of the belief among the miners that influenza either resulted from the eating of warty potatoes or was in some way transmitted from the potato to man. It is not difficult to account for the belief that warty potatoes might contain a poison which when eaten would cause influenza. Everyone is familiar with the fact that sickness and even death may result from the eating of poisonous mushrooms. It is more difficult to account for the origin of the idea that potato wart and human influenza might be one and the same disease. No infectious disease of plants has yet been found which is transferable to man or to animals. Likewise, no infectious disease of animals has been shown to go to plants. Therefore, none of the similarities which may be observed between the communicable diseases of the vegetable kingdom and those of man and animals results from identity of causative agents.

In its earliest stages of development phytopathology was little more than a branch of mycology. Plant pathologists concerned themselves almost entirely with the diseases caused by fungi. It was, in fact, believed that protozoa and bacteria were incapable of causing diseases in plants. Even at the present time phytopathology is treated as a part of mycology by some colleges and un-

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iversities. This is especially true of institutions in European countries. During the years when phytopathology was passing through what might be called its mycological period of development, students of human and animal pathology were busily engaged in studies of diseases caused by filterable viruses, protozoa, and bacteria, especially the latter. They gave relatively little attention to those caused by fungi. It is not surprising, therefore, that few similarities were observed between the diseases of plants and animals in this period. The causal agents of the diseases studied belong to different genetic groups

In more recent years phytopathologists have studied diseases due to infectious agents other than fungi. Since Burrill's (2) discovery that pear blight is due to bacteria, hundreds of other bacterial diseases of plants have been described. In 1909 a protozoan, Leptomonas davidi, was found in the latex of a Euphorbia (17). We now know that similar organisms infect the laticiferous cells of many different plants. Last year the Surinam wilt disease of coffee was found to be associated with a protozoan parasite of phloem tissues (27). Likewise, much attention has been given in recent years to studies on the virus diseases of plants. We now know that all of the different kinds of infectious agents which cause disease in man and animals also cause disease in plants. As work on the diseases of plants due to bacteria, protozoa and filterable viruses progresses, similarities between these diseases and animal diseases due to related, though not identical, agents become increasingly evident.

Anyone familiar with research work on viruses will readily think of many similarities between the diseases which affect plants and those which attack animals. The viruses of both groups are filterable and multiply only in living cells. They are capable of attenuation and are inactivated by heat or poisonous substances. No virus in either group has been proved to arise de novo, and none has been cultivated in vitro. The chief object of this lecture is to point out a few other similarities existing between the virus diseases of plants and diseases of animals. Special attention is invited to a consideration of similarities observed in studies on insect relationships, intracellular pathology, and immune reactions.

The phenomenon of insect transmission of disease is well known in plant pathology. Every plant virus disease which has been sufficiently studied has been shown to be carried by one or more insects. This means of spread is equally well known to animal pathologists. But it is in the field of plant viruses that insect relationships to disease transmission have been most carefully studied. Let us consider the nature of some of these relationships.

Certain virus diseases are highly infectious. It may be presumed that they can be carried in a mechanical way by almost any insect capable of feeding on susceptible plants. If a specific relationship exists between such a disease and any one insect, it is difficult to show because of mechanical transmissions. Such diseases are laboratory favorites. They can easily be taken out of their natural environments and short-circuited from plant to plant. This gives a splendid opportunity to study their symptoms, to prove they are due to filterable agents, and to determine the various properties of these agents. It is not so favorable for a study of their behavior in nature. Diseases which cannot be transmitted mechanically, or are difficult to so transmit, are much more favorable for this work. Practically all of our knowledge of the intimate relations of insects to plant viruses comes from work on diseases that are not highly infectious.

A few of these diseases are spread by two or more different insect species. Most of them, however, are transmitted by one insect only. They are, on the whole, far more specific for insect vectors than for host plants. This is well illustrated by such diseases as curly top of sugar beets, aster yellows, and grass mosaic. The curly top disease is reported to go to some sixty different species belonging in sixteen different families of plants (3, 24, 25). It is known to be transmitted by only one insect, the leafhopper Eutettix tenellus Baker. A large number of other insect species, including leafhoppers, feed on one or more of the sixty different kinds of plants which take curly top. Not one of these has been shown to transmit the disease. Aster yellows is known to go to 170 different species belonging in 28 different families of plants (16). A very large number of insect species feed on these plants, but only one, the leafhopper Cicadula sexnotata Fall., has been found which can

transmit the disease. Grass mosaic goes to a number of species in the grass family (13). Many different insects, including several kinds of aphids, feed on these plants, but only the corn aphid, *Aphis maidis* Fitch, is known to transmit the disease (1).

Further evidence of specificity in these disease and insect relationships is obtained from work on plants susceptible to more than one insect-borne disease. The sugar beet takes both curly top and a mosaic disease. The beet leafhopper which carries curly top is unable to transmit mosaic. The peach aphid which carries mosaic to beets does not transmit curly top. Likewise, the corn aphid which carries grass mosaic to corn cannot transmit the corn mosaic carried by the corn leafhopper, *Peregrinus maidis* Ashm. (11). This leafhopper, on the other hand, does not transmit grass mosaic. It is evident that the ability of these insects to spread disease is not dependent on any special relationship between them and the plants on which they feed. The specificity observed is between the insect and the disease.

The leafhopper Balclutha mbila Naude transmits the streak disease of corn (28). Not all individuals, however, are capable of carrying the disease. Storey showed that only about one-fourth of the males pick up the virus, whereas about 86 per cent of the females become infective. There are transmissive and non-transmissive individuals. Linford (18) found that only nymphs of Thrips tabaci Lind. can pick up the virus of the yellow spot disease of pineapples. Adults do not become infective by feeding on diseased plants. Adults can, however, transmit the disease if they develop from nymphs which have had an opportunity to feed on such plants. It was found that all individuals of the leafhopper Cicadula sexnotata are capable of picking up and transmitting the aster yellows virus (15). Many individuals carry and transmit the disease as long as they live. Others, however, transmit for a short period and then give no further evidence of having had the virus.

Even more convincing evidence of specificity is obtained from studies on the incubation periods of virus diseases in their vectors. Half a dozen well established cases are known in which vectors are unable to transmit virus diseases immediately after first feeding on a diseased plant. A definite period must elapse between the time when they first feed on the diseased plant and the time when they are first capable of transmitting the disease. In most instances these periods vary from a few hours to a day or more. Aster yellows has the longest incubation period which has been found to date. At temperatures most favorable for transmission, the virus of this disease has a minimum incubation period of ten days in the aster leafhopper. At lower temperatures which are more favorable for the growth of aster plants, the incubation period is about two weeks. The existence of such a long period suggests that the virus passes through a stage in its cycle of development in the body of the insect. This may account for the readiness with which the vector transmits aster vellows, a disease which cannot be transferred mechanically except by grafting. These examples show the intimate and peculiar relationships which exist between a few well known virus diseases and their insect vec-The rather complicated relationships suggest that so-called biological carriers of the virus diseases of plants may be necessary for the complete development of the agents causing these diseases.

In order to understand periodic outbreaks, seasonal occurrences, and other features in the epidemiology of these diseases, it is necessary to know their insect vectors and to determine how these vectors are affected by weather conditions, fungous diseases, parasitic and predaceous insect enemies, and various other environmental factors which limit or promote their development. It is important to know whether the vector produces one, two, or more generations a year. It is equally important to know in what plant species, wild or cultivated, the disease passes the winter. This knowledge is necessary in order to predict severe outbreaks and to control them.

You have probably noted similarities between the insect relationships here described and those known for certain virus diseases of animals. The rôle of leafhoppers and aphids in the spread of plant viruses is similar to that of mosquitoes in the spread of certain animal diseases. The incubation period of aster yellows in its leafhopper vector is similar to that of malaria in mosquitoes.

The most superficial observations on the intracellular symptoms

of plant and animal virus diseases bring evidence of similarities between these diseases. Affected cells of both plants and animals may be stimulated to such an extent that overgrowths are produced. They may, on the other hand, be killed. Necrotic lesions may then develop. Other common effects, such as enlargement or malformation of nuclei and the accumulation of crystals or deepstaining granules in the cytoplasm, may be noted. A most striking point of similarity is seen in the inclusion bodies found in the cells of plants and animals having certain virus diseases. In 1903 Iwanowski (8) described amoeboid bodies which he observed in cells of plants having the tobacco mosaic disease. In the same year Negri (22) reported somewhat similar bodies in the brain cells of animals having rabies. Following the publication of Negri's paper, cytoplasmic and nuclear inclusions were found to be associated with a considerable number of different virus diseases of animals. Iwanowski's observations regarding intracellular inclusions of tobacco mosaic remained unconfirmed and apparently unnoticed for a score of years. In connection with studies on a serious disease of sugar cane prevalent in the Fiji Islands, Lyon (20) in 1910 described inclusion bodies found in galls of phloem tissues. He believed the bodies to be parasitic organisms, but was unable to determine to what group they might belong. The malady studied by Lyon is a systemic gall disease which undoubtedly belongs in the virus group. In 1921 Kunkel (10) described inclusion bodies associated with the mosaic disease of corn and noted the similarity between these bodies and those associated with some of the virus diseases of animals

During the past ten years much attention has been given to studies on the intracellular bodies of plant virus diseases. These studies show that bodies are associated with many, but not all, virus diseases of plants. They have been described for tobacco mosaic (8), sugar cane mosaic (14), Fiji disease of sugar cane (20), corn mosaic (10), wheat mosaic (21), Hippeastrum mosaic (12), Brassica mosaic (20), Dahlia mosaic (6), Aucuba mosaic (26), and a number of other virus diseases. They have not been found in association with cucumber mosaic, Petunia mosaic, raspberry mosaic, clover mosiac, and many other virus diseases of plants.

Careful cytological work on a number of the Solanaceous host species of cucumber mosaic has not revealed inclusion bodies. Several of these species are susceptible to tobacco mosaic and show inclusions whenever infected with this disease (7). There are, therefore, excellent reasons for believing that if bodies were associated with cucumber mosaic they would have been discovered.

The inclusion bodies of the several different plant virus diseases studied vary considerably in size and shape. They also vary in structure and staining reactions. They often show deep-staining granules, and usually contain vacuoles. Those associated with each disease are sufficiently different from the inclusions of other diseases to be of diagnostic value. They are, on the other hand, enough alike to justify the conclusion that they are closely related structures. They are also sufficiently like the inclusions of certain animal virus diseases to suggest that they are of similar origin and significance. The intracellular pathology of plant virus diseases is remarkably like that of animal virus diseases in respect to the occurrence and development of inclusion bodies.

It has long been held that nothing comparable to acquired immunity in animals exists for plants. Such claims as have been made for acquired immunity in plants either lack confirmation or have been disproved. This has fostered the belief that a wide gap exists between plant and animal diseases in the field of immunity.

Price (23) has recently shown that tobacco and three other species of *Nicotiana*, *N. langsdorffi*, *N. sylvestris*, and *N. quadrivalvis*, acquire immunity to the ring spot disease. Ring spot is a highly infectious malady prevalent in the tobacco fields of Virginia and other southern states (5). It is caused by a filterable virus. The leaves of diseased tobacco plants bear chlorotic and necrotic spots having the Liesegang pattern.

About three days after inoculation of leaves by means of needle pricks or other methods involving slight wounding, primary lesions develop at the points where wounds were made. About three days later numerous ring spots appear on young leaves near the top of the plant, as is shown in figure 1. This is the systemic form of the

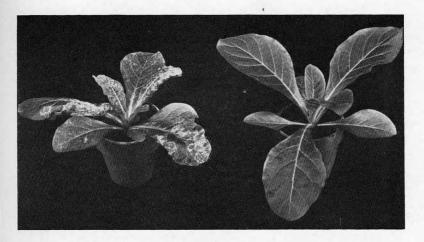


Fig. 1. Two plants of Nicotiana sylvestris. The plant on the left which shows the typical symptoms of ring spot was inoculated two weeks before the photograph was made. The plant on the right was not inoculated and is healthy.



Fig. 2. A recovered plant of *Nicotiana sylvestris* 37 days after inoculation with ring spot. All of the young leaves are •f a normal green color. Lesions may be seen on some of the oldest leaves.



Fig. 3. Cuttings from the plants shown in figure 1. The cutting on the left is from the plant which had the disease and recovered. The cutting on the right is from the plant which did not have ring spot.

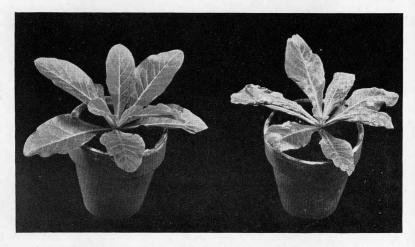


Fig. 4. Plants grown from the cuttings shown in figure 3. Photograph was made two weeks after both were inoculated with ring spot. The plant on the left which was grown from a cutting of a recovered plant is immune; the plant on the right which was grown from a cutting from a healthy plant has the disease.

disease. After a period of time varying from one to five weeks, depending on age, rate of growth, and environmental conditions, the plants regularly recover. A recovered plant is shown in figure The new leaves produced are of a normal green color, and are healthy in appearance. After a few weeks the leaves bearing spots mature and die. It is then impossible to distinguish plants which have had the disease and have recovered, from plants which have never been attacked. If, however, plants which have recovered and plants which have never suffered an attack are inoculated with the virus of ring spot and held under the same conditions, the two sets of plants will be found to react very differently. covered plants remain normal and healthy in appearance. Neither the primary nor the systemic form of the disease develops. The plants that have not previously had the disease come down with a severe attack. Price propagated from recovered plants through several generations by means of cuttings like those shown in figure The plants produced in this way are immune to ring spot, while similar plants propagated in the same way but from individuals which have never had ring spot are highly susceptible, as is shown in figure 4. It is possible, through the control of environmental conditions, to cause a mild attack of ring spot. After recovery from such an attack plants are immune under a wide range of conditions, including those which favor a severe attack of the disease.

It must be mentioned that the virus of ring spot is recoverable from all plants which have suffered an attack. It can also be obtained from plants grown through several generations from cuttings from recovered plants. Most seedlings from the seeds of recovered immune plants do not carry the virus and are susceptible to ring spot. A few which do carry the virus are immune.

The essential facts regarding this disease, insofar as they are at present known, may be summarized as follows: The four *Nicotiana* species studied by Price are highly susceptible to ring spot. When inoculated with the virus they suffer an acute attack of the disease. A systemic form of infection follows the development of primary lesions. Plants regularly recover and are then immune. They never suffer a second attack. The virus is retained by and recover-

able from all plants which have had the disease. Tobacco seedlings from seeds of recovered plants are immune if they carry the virus, but susceptible if they do not (29).

This acquired immunity to ring spot in *Nicotiana* differs from most cases of acquired immunity in animals only in respect to the retention of the causal agent by recovered individuals. In most cases the agent causing the disease to which an animal becomes immune is not recoverable after the disease subsides. There are, however, instances in which the causal agent persists. Infectious anemia of horses (9), the salivary gland disease of guinea pigs (4), and contagious epithelioma of chickens (19) are examples of non-sterile immunity for virus diseases in animals. Immunity in these instances is similar to that in *Nicotiana*.

I have attempted to describe some of the peculiar relationships which exist between plant virus diseases and their insect vectors, and to point out that in certain respects these relationships are similar to those existing between animal diseases and the insects that transmit them. It is suggested that further studies on these relationships for both plant and animal diseases may reveal other similarities. I have tried to describe very briefly some features in the intracellular pathology of plant virus diseases. Inclusion bodies resembling those occurring in the cells of animals having certain virus diseases are associated with a number of the virus diseases of plants. Other virus diseases of plants are not accompanied by the production of inclusion bodies. A like situation exists for the virus diseases of animals. Finally, I have attempted to show that, even in the field of acquired immunity where plants have been thought to differ so widely from animals, there are close similarities such as have been observed for the ring spot disease of tobacco in four species of Nicotiana.

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