AN ABSTRACT OF THE THESIS OF

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Title A study of viruses affecting European and American potato varieties.

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Virus diseases of potato have during the years been described independently in Europe and America. Thus different nomenclatures have developed in various countries often resulting in (1) several names for the same disease, and (2) confusion in identity. The symptoms of a disease may vary on different potato varieties. It was the purpose of the researches reported in this thesis to bring together these viruses and study them under uniform conditions to establish universal identity and eliminate duplication in nomenclature.

As a result, the chief symptoms, as found in different American and European potato varieties and some other solanaceous plants, are described for mild mosaic, crinkle mosaic, crinkle, leaf-rolling mosaic, para-crinkle, vein-banding, Y virus, stipple streak, X virus, top necrosis, B virus, top necrosis C virus, tuber blotch, pseudo-net necrosis, Aucuba mosaic, Canada streak, and Calico.

The relationship existing between different viruses has been determined on the basis of (1) similarity of symptoms in

different host plants, (2) by protective inoculation, (3) serological similarities, and (4) by studying the relation of certain physical properties of viruses (such as longevity *in vitro*, dilutions, and the thermal inactivation point) to infectivity.

Mild mosaic, crinkle mosaic, and crinkle were found to be so similar in many respects that although they are not identical they are so closely related that the component in addition to X found in the virous complex causing each of the three diseases, is designated as "A".

Leafrolling mosaic was found to be distinct from para-crinkle. The virus in the complex, in addition to X, is designated as "B".

Veinbanding, Y virus, and stipple streak vary somewhat in the severity of symptoms produced in different hosts, but the general type of symptoms are similar. Serological and property studies prove that they are closely related strains of the same virus, and all three are designated as "Y".

No relationship was found between the veinbanding and cucumber-mosaic virus on the basis of inoculations in potato and tobacco. None of the Y viruses protected against infection of cucumber mosaic in tobacco.

Amaranthus rectoflexus was found to be a host of X virus.

D virus proved to be an aberrant strain of X. Seedling 41956 was found to be immune from all strains of X virus tested.

B virus produces top necrosis in the varieties Arran Victory and President. Green Mountain was found to carry this virus in addition to X. It was not found in the varieties Bliss Triumph, Burbank and Earliest of All.

C virus causes top necrosis in all of the American potato varieties tested. The tuber-perpetuated symptoms in these varieties consist of a mottling. Grafts of scions from such plants to healthy potatoes produce a mottling instead of a top necrosis.

Pseudo-net necrosis and tuber blotch were found to be identical, and this virus is designated as "p".

Canada streak is a strain of Aucuba mosaic, producing necrotic spots in the parenchyma of the tubers in every variety tested. This virus, the same as the one causing Aucuba mosaic, is designated as "g".

The Aucuba-mosaic group of viruses includes pseudo-net necrosis, Aucuba mosaic and Canada streak.

Calico on the basis of incomplete studies, does not seem to be related to the viruses of the Aucuba-mosaic group.

A STUDY OF VIRUSES INFECTING EUROPEAN AND AMERICAN POTATO VARIETIES

by

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TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

A STUDY OF VIRUSES INFECTING EUROPEAN AND AMERICAN POTATO VARIETIES

by

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INTRODUCTION

Progress in potato virous work is now considerably delayed, principally for want of an accepted system of virous recognition. The fact that the symptoms caused by viruses may vary considerably, depending upon the variety of the host plant, and that a number of diseases are found to be due to a mixture of viruses emphasizes the necessity of distinguishing between a virus and the type of disease it causes. That different potato varieties are used and a different system of nomenclature in regard to virous diseases is followed in Europe than in this country, accounts for the existence of the present confusion of the identity of the different viruses affecting potatoes on the two continents. In order to determine the identity of the viruses found here and abroad, diseased and healthy potatoes of different varietal types were secured from Europe and compared with the viruses on potatoes found in this country.

Since healthy tubers of European varieties are often free from the X virus (latent mosaic universally present in all of the older so-called "healthy" commercial varieties

in America), it was considered advisable for comparison of the viruses to remove the X component from the American as well as from some of the European virous complexes. This was readily accomplished by grafting scions of virus-diseased potatoes to the U. S. D. A. seedling 41956, which is immune from this latent virus (34). By this procedure it was possible to filter out the X and to retain in the seedling variety the other one or more components of the complex. These different virous components of European and American origin have been studied under identical conditions on different American and European potato varieties, in many cases on plants that came from the same tuber unit, as well as on other solanaceous host plants. In addition, some of the physical and chemical characteristics of these viruses have been determined.

These studies were started in the fall of 1933 at Corvallis, Oregon, and conducted in the greenhouse and under insect-proof cages in the field. A preliminary report on this work has already been published. (10, 11) In the spring of 1936 the writer was transferred to Beltsville, Maryland, where the studies were continued at the U. S. D. A. Horticultural Station.

Early Studies

The early work on the classification of the different potato viroses found in this country was conducted by Schultz and Folsom (35) and by Quanjer in Europe (26). In most of this work in the United States the variety, Green Mountain, was used. At that time it was not so fully realized that such a variation of symptoms of the same virus may develop on different potato varieties. It is now known that the symptoms caused by viruses are reactions of the host to the presence of the virus, and are influenced by factors that pertain to the host, such as species, variety, and environment. It is, therefore, not possible to develop a general system of classification on the basis of symptoms alone. The term "mild mosaic" for example, is applicable to the symptoms produced by a known virus in a number of varieties of potato; but at least in two varieties, namely Up-to-Date and British Queen, it produces a definite acronecrosis. The term "latent virus of healthy potatoes" originated when it was believed that this virus was latent in all potato varieties. We know now that this virus causes a definite mosaic-like mottling in some varieties like President and Arran Victory, and a severe top necrosis in the varieties Epicure and Katahdin.

Whereas formerly a system was developed only to classify the diseases caused by the different viruses, the need is now felt for a classification of the different viruses causing the diseases. Johnson (16) attempted to identify and differentiate potato viruses by the determination *in vitro* of certain physical and chemical characteristics to which he referred as the "properties" of the viruses. He considers the most reliable diagnostic features of the "property" type, the thermal death point, the longevity *in vitro*, the effect of dilution, and the influence of certain chemicals. Quanjer (27), although agreeing that the determination of these properties offers great possibilities for acquiring knowledge of the nature of the viruses concerned, believes that such studies cannot be expected to give much information on their properties as pathogens. He states that our knowledge of the virous diseases of plants has been secured by the following methods:

A. Indirect methods ("pathological methods" according to Quanjer):

   1. Study of symptomatology
   2. Study of the morbid anatomy and physiology of the host
   3. Determination of the host range
   4. Determination of the modes of transmission and of the relation between vectors and viruses

5. Determination of the effect of environment on the host

B. Methods not yet classifiable as direct or indirect:

6. Chtological studies

C. Direct methods ("property methods" according to Johnson):

7. Cultivation of the viruses and determination of their physical and chemical characteristics.

Quanjer follows the principle that a potato virus should be identified, named, and classified according to the morbid effect it has on a variety that shows clearly, defineable, internal symptoms. He considers President one of the best differential hosts. To avoid further trouble resulting from the use of descriptive names for an ever-increasing number of mosaics, crinkles, and streaks, he suggests the following as an international system of nomenclature for the potato diseases of the virous type.

Anecrotic mosaics; producing only mottling and more or less wrinkling of leaflets, without necrosis.

Acronecrosis (or top necrosis); necrosis radiating from only a rather small percentage of the internal phloem strands, into the surrounding parenchyma.

Acropetal necrosis; necrosis chiefly in the collenchyma of the leaf veins, petioles, and stems extend-

ing gradually to other tissues. Dropping of lower leaves.

Phloem necrosis; necrosis restricted to the phloem strands, i.e., sieve tubes and companion cells, accumulation of carbohydrates in the leaves.

Phloem parenchyma necrosis (pseudo net necrosis); necrotic spots in the storage parenchyma next to the external and internal phloem of the tubers only.

Bawden (3) although realizing that these histopathological changes offer a promising field for research on the pathogenicity of viruses, fails to understand the advantage gained in using the morbid anatomy of infected plants as criteria for classification rather than the external symptoms, which he considers more definite and recognized with much greater ease than the internal changes. He finds that the virus causing a leaf-drop streak (Acropetal necrosis) in President produces a mild crinkle in Arran Victory, while that causing a lethal top-necrosis streak in President produces a still more mild crinkle in Arran Victory. Corresponding to this varietal expression of any given virus is the histopathological picture induced: Where in the infected plant external necrotic changes occur, be it of the acropetal or acro-necrotic type, so in the tissues will be found the corres-

ponding histological characters, a necrosis of the supporting collenchyma in the one case, that of the phloem groups in the other. When in the plant the virus produces only a crinkle mosaic, while (in such cases) in the tissues of the stem and petiole no necroses are to be found.

In 1931 Smith (36) started the alphabetical system of nomenclature, when he designated, as X, the virus causing the disease known in Europe as simple mosaic, and as "latent mosaic of healthy potatoes" in America. He called the virus causing acropetal necrosis, the common leaf-drop streak in President, "Y". Murphy and McKay (1932) (20) described virus "A" which they found occurring alone in healthy appearing plants of the variety Irish Chieftain, and which in addition to the virus X causes the potato disease known as crinkle. Bawden (unpublished thesis Smith's book (37, 3) described virus "B" which seems almost universal in the variety, Up-to-Date, which carried it without symptoms, but usually accompanied by X virus. B virus, when transmitted by grafting produces a top necrosis in several varieties. Bawden (3) also described a C virus as occurring in the variety Di Vernon. Scions from infected Di Vernon when grafted to virus-free Arran Victory and President plants, produce top necrosis in the latter, while the former reacts with mosaic

symptoms only. The non-production of top necrosis in Arran Victory differentiates this virus from B virus. D virus (4) has also been described by Bawden. This virus causes top necrosis in a variety of potatoes, all of which either carry virus X or show only interveinal mottle when infected with it. Clinch, Loughnane & Murphy (9) designate the virus causing tuber blotch as F, and the one of Aucuba mosaic of potato is designated as potato virus G. These authors by taking a general view of their properties and reactions, classify the potato mosaic viruses into three broad groups, namely:

1. Viruses of the X type, which cause distinctive mosaic symptoms in many solanaceous hosts, form crinkle when combined with A virus in potato varieties tolerant of that disease, and are non-transmissible by Myzus persicae.

2. Viruses of the F type (tuber-blotch virus) which produce characteristic brown or purple fringed spots on Solanum nodiflorum, produce typically bright yellow spotting of the lower leaves of potatoes, which is intensified by the presence of virus A, and cause hereditary parenchyma necrosis in the tubers of many potato varieties.

3. Viruses of the Y type, which are readily transmissible by Myzus persicae, produce veinbanding in

tobacco, are non-inoculable to Datura stramonium, and typically cause acropetal necrosis in certain potato varieties, although this feature varies in the case of virus A.

Technique Used in Transmission of Viruses

Various means of transfer of the several potato viruses were tried out. Certain methods were successful with some of the diseases while not so satisfactory with others.

Leaf mutiliation: In this method, as described by Schultz and Folsom (35), cheesecloth soaked with the juice from macerated foliage of diseased plants was rubbed on the leaf of a healthy plant, enough pressure being used to break the trichomes, the epidermis, or mash or mutilate to a degree the tissues. This method was successful in transmitting many of the viruses, but there was considerable variation in the amount of infection of different viruses secured by this method. It was later found that the percentage of infection of those viruses which are transmitted with difficulty could be increased by adding a small amount of carborundum dust to the inoculum (30). This acted as an abrasive and facilitated the entrance of the virous particles into the inoculated plant.

Stem grafts: It was found that with the exception of the veinbanding or Y group of viruses, the grafting method of transferring the different viruses was far more successful than the leaf mutilation method. Stem grafts of diseased scions were made to potted healthy plants, which were kept in a moist chamber for about 10 days. Then they were removed and kept in the greenhouse for further observations, according to the method recommended by Salaman and Le Pelley (31). When this procedure was followed, about 80% of the grafts were successful.

Acquired immunity of plant viruses: Several workers namely Thung (39), Price (24), Holmes (13), Salaman (33) and others, have found that there are different strains of viruses causing diseases, which show considerable degree of difference in severity. They found that plants infected with one strain are often thereby protected against infection by other strains of the same virus, including those of greater severity. To determine whether or not some of the different potato virous diseases are caused by strains of the same virus, or by unrelated viruses by this means has also been used in the studies recorded here.

Serological Studies: Beale (5), Chester (7), and others have carried on serological experiments demonstrat-

ing that the injection of rabbits with plant-virus extracts induces in such animals the production of antibodies. When the serum from the animal containing the antibodies is added to juice from a plant containing the same virus, or that of a related strain the soluble antibody of the serum and the soluble antigene of the virous juice combine to form an insoluble precipitate, which slowly settles out. Unrelated plant viruses fail to react. It is believed that this method provides a very useful means of determining the relationship between different potato viruses. Accordingly, a number of these viruses have been tested serologically through the courtesy of Dr. K. Starr Chester, formerly of the Rockefeller Institute at Princeton, N. J.

Sources of the Viruses Studied

In 1924 tubers of the Green Mountain variety infected with mild mosaic, leaf-rolling mosaic, crinkle mosaic, and rugose mosaic were furnished to the Oregon Experiment Station by Dr. E. S. Schultz of the U. S. Department of Agriculture from the experimental stocks grown at the field station at Presque Isle, Me. Since then material has been propagated on different varieties under muslin-covered cages in the field, and constituted the source of the American viroses of potato used.

In 1933 Y virus in President, Crinkle A in

in President, Para crinkle in Arran Victory, Virus C in Di Vernon, the B virus in Up-to-Date, and healthy tubers of President, Arran Victory, and Majestic were secured from Dr. R. N. Salaman of the Potato Virus Institute of Cambridge, England. In 1936 interveinal mosaic, and the blotch virus in the variety President were received from Dr. P. A. Murphy of Glasnevin Agricultural College, Dublin, Ireland. At that time stipple streak in Zeeland Blue, pseudo-net necrosis in President, and healthy tubers of British Queen were received from Dr. H. M. Quanjer of the Agricultural College, Wageningen, Netherlands.

Studies on Individual Virous Diseases

The discussion of the individual diseases brings together the results of observations and experiments conducted by the writer. The symptoms are described as those met with under greenhouse conditions which were kept mainly at a temperature varying from 65° to 75° F.

The number of plants used in the different experiments is not always stated, but with the exception of a few cases mentioned in the text, a sufficiently large number of plants, generally not less than 20, were used in each test to make the results significant, and similar inoculations were often repeated.

Mild mosaic: This disease was originally described by Schultz and Folsom (35). It is composed of at least one component in addition to X. The symptoms in Green Mountain are characterized by a mottling in the green of the leaf in which yellowish or light-colored areas alternate with similar areas of normal green. This is usually accompanied by a crinkling but not a rolling of the foliage. These mottled areas are variable in size and shape and located without regard to the different tissues such as the veins of the leaf. This is in contrast to the loss of color occasioned by other factors than mosaic which may give rise to yellowish, somewhat circular, island-like areas of the leaf tissues between the larger veins. In mild mosaic the lighter colored areas are not bounded or stopped by leaf veins. Diseased plants droop and die prematurely. No symptoms are evident in affected tubers. This disease has been studied in the American varieties, Burbank, Earliest of All, White Rose, and Bliss Triumph. The symptoms in these varieties although varying slightly in intensity depending upon the variety, are not fundamentally different from those described in Green Mountain. By grafting scions of infected Green Mountain on Seedling 41956, immune from the latent virus, the X virus was eliminated and the other

component was retained. This component has been studied in the European varieties President and Majestic, alone and in combination with X. Whereas the component alone free from the X causes a very faint mottling, a very pronounced mottling and crinkling of the foliage was evident when the X virus was added to it. This virus has also been transmitted by grafting scions of infected 41956 to six Up-to-Date and to ten British Queen plants. All grafted plants became infected and developed typical top necrosis, manifested by the dying of the top part of the plant and the development of rather large necrotic blotches on the top and intermediate leaves. No mottling was evident.

Mild mosaic-X has been transmitted to tobacco plants. One hundred per cent infection was often secured when the juice extracted from the leaves of an infected plant was rubbed lightly on the tobacco leaves by means of a cotton swab on the surface of which was a small amount of carborundum dust. The symptoms on tobacco consist of a mottling which resembles the mild mottling sometimes produced by the X virus. It was found that it can be readily distinguished from this virus, by inoculating infected plants with tobacco mosaic. The tobacco plants infected with the X virus upon addition of tobacco mosaic will invariably develop a spot necrosis on the leaves,

whereas the plants infected with the other viruses will develop only tobacco mosaic symptoms in addition to the mottling due to the particular potato mosaic virus present. The presence of mild mosaic on tobacco was demonstrated by making return inoculations to Bliss Triumph and Green Mountain, to which the disease was again transmitted. This virus has also been transmitted to Nicotiana sylvestris in which it developed fairly distinct symptoms consisting of small yellow patches following the veinlets.

Crinkle mosaic: This disease was originally described by Schultz and Folsom (34). It is composed of at least one component in addition to X. On Green Mountain it is characterized by a prominent mottling and crinkling of the leaflets. It differs from mild mosaic in that the leaflets are more ruffled and the blotches are larger. This disease has also been studied on the same varieties to which mild mosaic was transmitted, namely Burbank, Earliest of All, White Rose, and Bliss Triumph. The symptoms on all these varieties are more intense under the same conditions than those caused by mild mosaic. About the same percentage of this disease is transmitted by leaf mutilation as in the case of mild mosaic. By grafting scions of infected Green Mountain to seedling 41956, the X virus was eliminated and the other component retained. This has also been studied on the European

varieties, President and Majestic, alone and in combination with X. The same as in the case of mild mosaic, the component alone caused a faint mottling and a much more pronounced mottling and crinkling of the leaves was evident when the X virus was added to it. Crinkle mosaic X produces symptoms on tobacco indistinguishable from those caused by the mild mosaic component.

Crinkle: This disease is well known in Europe and has been described as crinkle by Murphy (22), Quanjer (26) and Salaman (32), the last of whom refers to it as crinkle A to distinguish it from para crinkle. It is composed of at least one virus component in addition to X. The presence of X was indicated by the interveinal mottle and vein-clearing it produced in Datura stramonium, and the ring-spot type of mottle on tobacco. The disease has been transmitted to the American varieties, Green Mountain, Bliss Triumph, Earliest of All, and Burbank. In all these varieties it produced a mottling and crinkling of the leaves very similar to those produced by mild mosaic. By grafting scions of infected President to seedling 41956, the X virus of the complex was eliminated. The remaining component referred to by Murphy as Crinkle A has been transferred to President and Majestic causing a faint type of mottling. When the X virus was added to it the mottling and crinkling were considerably intensified and were more

prominent in President than those caused by mild mosaic. The symptoms of A virus are indistinguishable in tobacco and Nicotiana sylvestris from mild mosaic and crinkle mosaic component free from X. Murphy and McKay (22) showed that A virus produces a necrotic disease in Up-to-Date, and Clinch and Loughnane (8) confirmed this showing that it also produces top-necrosis in British Queen. Their results were confirmed when 4 Up-to-Date plants and 4 of the British Queen variety were grafted with scions of 41956 infected with the A virus. Everyone of the plants grafted developed typical top necrosis, showing symptoms very similar to those produced by the transmission of mild mosaic-X to the same varieties.

The results secured on the basis of relative ease of transmission, symptoms produced, and the general behavior of these three viruses, namely mild mosaic, crinkle mosaic, and crinkle, indicate that although the viruses causing these three diseases are not identical, they are so similar in their behavior that they may be considered to be three closely related strains of the same virus. It is proposed, therefore, that the viruses causing these three diseases be designated as "A".

Leaf-rolling mosaic: This disease was originally described by Schultz and Folsom (35). The mottling of the leaflets of Green Mountain plants infected with leaf-rolling

mosaic is diffused and resembles the type found in rugose mosaic. The leaves generally show a rolling upwards, but the leaves are flaccid and resemble the type of rolling found in plants affected with Rhizoctonia or blackleg. This disease has also been studied on other varieties. The rolling and mottling is almost masked in Burbank and Irish Cobbler, but the symptoms in varieties like Earliest of All, Idaho Rural, Bliss Triumph, and White Rose are quite similar to those of Green Mountain. Leaf mutilation has given a fair percentage of infection, about the same as secured with mild and crinkle mosaic.

Leaf-rolling mosaic, free from the X virus, as well as the complex leaf-rolling mosaic and the X virus, have been transferred to the English varieties, President and Arran Victory. The symptoms of these diseases in these two varieties are characterized by a diffused mottling and rolling of the leaves. The addition or the absence of the latent virus did not appear to influence the symptoms appreciably. All attempts to transmit this virus to tobacco failed. The disease appears to be distinct from any of the other American or European potato viruses which were studied, and it is proposed that the virus causing this disease be designated as "E".

Para crinkle: This disease was first described by Salaman and Le Pelle (31). They found this virus to be

universally present in the variety King Edwards, which appears to be a perfect carrier of this disease, since no symptoms can be detected in it. They observed that when this virus was introduced by grafting into Arran Victory it induced a severe disease, but when infected by the same method in President, failed to produce the slightest reaction. The virus, however, could be recovered from President, by making return grafts to Arran Victory. In a later paper (32) Salaman stated that para crinkle consisted of a complex of Z and Y^1, and that passage of the para crinkle complex through a Datura with leaves will break down the complex and remove one of its constituents, namely Y^1. Later in conversation Dr. Salaman stated to the writer that he no longer held that view, and believed that para crinkle was due to the effect of a single virus component. We found that para crinkle could not be transmitted by juice transfer, but was readily transmitted by stem grafting. It was transmitted to the varieties, Burbank, White Rose, Earliest of All, Bliss Triumph, and Green Mountain. In these varieties it produced large mosaic-like blotches on leaves, but failed to produce any crinkling or rolling. In the variety Burbank, pin-point like necrotic spots developed in the leaves in addition to the mottling when infected

tuber-perpetuated plants were grown under cages in the field. This disease was also transmitted by grafting to tomatoes and produced a somewhat filiform type of leaf, return grafts from infected tomato to Arran Victory reproduced the disease. Murphy and McKay (21) have suggested that this virus may have affinities with leaf-rolling mosaic. The writer has studied this disease in comparison with leaf-rolling mosaic in the American varieties, Burbank, White Rose, Earliest of All, and Bliss Triumph, and on the European varieties, President and Arran Victory, but no resemblance of the symptoms of these two diseases was detected. Whereas leaf-rolling mosaic can be transmitted by juice transfer, all attempts to transmit para crinkle by this method failed.

Veinbanding virus: The rugose mosaic of potato which was described by Schultz and Folsom (35) is due to a combination of the latent, or X, and veinbanding viruses. It is the aphid-transmitted component of rugose mosaic, according to Koch (17). This virus has been studied in the American varieties, Green Mountain, Earliest of All, Irish Cobbler, Bliss Triumph, White Rose, and Burbank. There is very little variation in the symptoms produced by this virus in these different varieties and they consist of small mottled areas, grouped close to the main veins. During high temperature the mottling may be completely masked, but the crinkling of the leaves and their tendency

to curl slightly downward persists. Some of the veins of the lower leaves generally are necrotic, resembling black, pencil-like lines. The affected plants are noticeably stunted and generally die prematurely. In contrast with most of the other potato viruses, the symptoms due to current season infection are different from the ones produced the succeeding years, due to tuber perpetuation of the disease, and in many varieties consist of a burning or necrosis of the veins of the newly developed leaves and a dying of the tissue between the veins. These leaves will eventually drop, or hang on by a thread of tissue of the stem. In the European variety President it produces a mottling in the top leaves and some necrosis, especially in the intermediate leaves but in the second generation only a diffused mottling of the leaves was evident, but practically no necrosis of the veins or leafdrop. In Arran Victory a diffused mottling, but without any necrosis or leafdrop, developed. Only a diffused mottling was noticed in infected Epicure. In tobacco this virus produces a banding of the veins and during the later stages of the disease a general mottling develops in the leaves. In tomato no symptoms were evident except a faint clearing of the veins. This virus produced a banding of the veins in pepper, later changing into a mottling. In infected petunia plants a faint

vein-clearing of the leaves was evident, and distinct mottling developed in the petals of the flowers.

Y virus: Smith (36) originally described virus Y as one of the commonest and most destructive of potato viruses in England. The symptoms caused by this virus have been studied in a number of American and European potato varieties. After an incubation period of fifteen to twenty days a blotchy mottle appears in the variety President, spreading from the veins and affecting the uppermost leaves only. This mottle later becomes intensified and is accompanied by some wrinkling and waving of the leaves. A little later necrosis appears on the under sides of the veins of leaves occupying an intermediate position on the stem. These necroses increase in severity and spread most rapidly along the course of the veins on the under surface of the leaf, appearing as elongated brown stripes on the petioles and as blotches between veins. The necroses pass down the petiole to the main stem and the leaf then collapses, rapidly withers and remains hanging by a thread. The stem often shows elongated brown stripes. In Arran Victory and Epicure the symptoms are only those of a mild mosaic mottling. The current season symptoms of the Y virus in Irish Cobbler, White Rose, Burbank, Bliss Triumph, Green Mountain, and Earliest of All, which also harbor X virus,

are manifested by necrotic leaf-spots including the veins and the tissue immediately surrounding them. Nearly every leaf on the plant may eventually drop, and remain hanging on the main stem by a thread of tissue, leaving only a tuft of leaves at the tip of the plant. Plants from tubers of plants infected with Y virus appear at first as if infected with rugose mosaic, except that the necrosis of the veins instead of being confined to the lower leaves, is found in almost every leaf. While the plant is still immature, the lower leaves at first green, gradually turn yellow and drop, but remain hanging on the stem by a thread of tissue. In the variety Bliss Triumph the petioles develop necrotic spots and stripes of streak are found on the stem. Finally, all the lower leaves dry down and hang on the main stem. At this stage of development the disease appears to be quite different from rugose mosaic. These observations were also made by Koch and Johnson (18) who state: "It appears certain, therefore, that Smith's virus Y, while possessing many characters in common with the American veinbanding virus, is not identical with it."

The Y virus in tobacco causes a distinct banding of the veins, which is later followed by a general yellowing between the veins; the symptoms are much more pronounced than those caused by the veinbanding mosaic.

Inoculations into Petunia failed to cause a mottling of the flower petals, whereas this generally was true with the veinbanding and stipple-streak virus. On pepper the symptoms were quite similar in pattern to those produced by the veinbanding virus, except that they were more pronounced.

In order to determine whether or not the Y virus has any effect upon potato plants infected with rugose mosaic the following experiment was started in the spring of 1935. Each of 6 tubers of the variety Green Mountain and 6 tubers of Bliss Triumph infected with rugose mosaic were cut into 3 pieces. Each seed piece was planted in a 6-in. pot in the greenhouse. When the plants were about 3 or 4 inches high, those derived from 1 seed piece of each tuber were inoculated with the Y virus by means of the rubbing method. Plants from another seed piece of each tuber were inoculated with the veinbanding virus, and the other seed pieces were not inoculated and served as controls. These plants were kept under observation for more than 2 months after inoculation, but none of the plants developed symptoms different from the controls, which showed the typical tuber-perpetuated rugose mosaic symptoms. This experiment showed that the veinbanding mosaic in the rugose mosaic complex had a protective effect which prevented the development of symptoms typical

of the Y virus in Bliss Triumph.

Stipple-streak: The stipple-streak virus was first described by Atanasoff (1) and is universally present in the Dutch variety, Zeeland Blue. Although the virus is masked under high temperature, this variety cannot be considered as a carrier, since a definite interveinal type of mottling is evident under low-temperature conditions. The tubers of Zeeland Blue received from Holland contained in addition to the stipple-streak virus, also a weak strain of X virus. Murphy and Loughnane (23) state: "It was formerly thought that the responsible virus in this material was Y virus, but more than one virus is present, and the analysis is not yet complete." Since Zeeland Blue has been growing as a commercial crop in Holland, it undoubtedly has contracted other viroses, but the writer believes that the typical symptoms in potatoes and other Solanaceous plants caused by stipple-streak are primarily due to the stipple-streak component, and not to a complex. In our tests with this virus, the X component was removed by inoculating juice from an infected Zeeland Blue into seedling variety 41956.

In many potato varieties, circular necrotic spots developed in the inoculated leaves, and necrotic spots, rather than burning of the veins, were found in the

intermediate uninoculated leaves.

The stipple-streak virus causes a banding of veins in tobacco leaves but the symptoms are more like those caused by the veinbanding virus than the Y virus. In Nicotiana sylvestris a definite veinbanding is observed, but the band following the veinlets is thinner than that caused by the Y virus. Infected plants show less rugosity than in the case of infection by veinbanding. nThe symptoms in Petunia were quite similar to those produced by the veinbanding mosaic, and a breaking of the petals of flowers of infected plants was evident.

The Y virus was inoculated into ten Zeeland Blue plants carrying the stipple-streak virus. These plants were kept under observation for a period of ten weeks, but no additional symptoms due to the Y virus were evident. When at the end of that period, juice from leaves of each of these 10 plants was inoculated into 20 tobacco plants, only the faint veinbanding characteristic of the stipple-streak virus developed. This showed that this virus protected the plants from infection with the Y virus.

The symptoms produced by the Y, veinbanding, and stipple-streak viroses vary in degree and intensity in the same potato varieties, but the type of symptoms produced is similar. In some varieties a mottling

develops, and in others an acropetal necrosis, but no instances have been observed where one of these viruses caused a mottling and another acropetal necrosis in the same variety. The same general symptoms have also been observed in other solanaceous plants, but in all cases the effect of the Y virus was the more severe. Dr. K. Starr Chester, as a result of serological studies, reported in a letter dated May 29, 1937: "The European strain of Y virus proves to be serologically indistinguishable from our ordinary veinbanding virus. Stipple streak also belongs to the veinbanding group." Dilution test, thermal inactivation point determination, longevity in vitro, effect of pH on viroses (Table I) protective inoculation studies, and serological investigations, all tend to prove that these three viroses are closely related strains of the same virus. It is proposed, therefore, to designate these three strains as Y virus.

Relationship between Cucumber Mosaic and Veinbanding

Chester (7) states as a result of his serological studies with different viroses that such a close serological relationship is shown between the veinbanding virus of potato and cucumber mosaic that one may well be justified in regarding these as strains of the same virous

type. This heretofore unrecognized relationship is further borne out by the fact that veinbanding and cucumber mosaic viruses each produce in the cowpea, Vigna sinesis (L.) Endl., local brown necrotic lesions that are indistinguishable in appearance.

To determine whether cucumber mosaic could be transmitted to potato, in 1936, 40 potato plants consisting of the varieties Green Mountain, Bliss Triumph, and some potato seedling varieties, were inoculated with extracted juice from infected cucumber plants. None of these plants developed symptoms, nor was it possible to recover the virus from inoculated plants by making return inoculations to tobacco.

The tubers from the inoculated plants were saved and 35 of these were planted in the greenhouse in the fall of 1937. These plants all appeared healthy, and when inoculated with the veinbanding virus developed symptoms typical of this disease, indicating that no virus was present in these plants to protect them against infection of the veinbanding virus. Ten potato plants were grafted with scions of cucumber-mosaic-infected tobacco plants, but these also failed to produce any symptoms. Three series of 10 tobacco plants each were inoculated respectively with the veinbanding virus, the Y virus, and stipple-streak. After symptoms had developed these

plants, in addition to ten healthy control plants, were inoculated with cucumber mosaic. All plants developed typical cucumber-mosaic symptoms and there was practically no difference in the time required for symptoms to develop in the four series of tobacco plants, showing that no protection against infection of the cucumber-mosaic virus was afforded by the presence of either the veinbanding, Y, or stipple-streak virus. On the basis of our inoculation studies, we must conclude that there is no relationship between cucumber mosaic and veinbanding.

X Virus

In 1925, Johnson (15) described the "mottle virus" which was shown to be regularly present, in masked form, in all tubers of most, if not all, standard varieties of "apparently healthy" potatoes. In Europe this disease, which shows a mild type of mottling in some varieties, has been described as simple mosaic (21). According to Murphy and McKay (21) it corresponds exactly to "common mosaic", as described by Quanjer (26), and it is identical with the "Arran Victory mosaic," of the Cambridge workers. Murphy (21) states "one of the latent viruses, commonly present in the American material, both diseased and healthy, was a necrotic form, identical with the common streak of Up-to-Date and other similar sorts." Murphy

apparently referred to the B virus, which will be discussed later in a different chapter. He goes on by stating, "another virus which, according to our experience, was even more common in this material was European simple mosaic. Certain American "healthy" plants were found which were apparently free from streak, but no such plants were free from simple mosaic." Kenneth Smith (36) designated the virus causing this disease as X. This virus is not always found in European varieties, although when the writer was in Europe during the summer of 1935, he was informed by different investigators, that the X virus is quite common in practically all varieties, and as much as 40 or 100% of some varieties may be infected with it.

The symptoms caused by X in Datura and tobacco are so well known that it will not be necessary to discuss these in detail. The writer has also transmitted this virus to Amaranthus rectoflexus, in which it produced necrotic spots on the leaves. The virus was readily recovered from infected plants by making return inoculations to Datura stramonium, in which it produced the typical X type of mottle. This is believed to be the only potato virus that has been successfully transmitted to plants outside of the Solanaceae.

It was interesting to note that seedling 41956 was immune from all strains of X virus, with which the writer has been working. Bawden (4) described virus D, which he places in or near the X group on account of the possession of a number of properties characteristic of X. Since this virus appeared to be so different from the other strains of X, a tuber infected with virus D received from Bawden, was planted and the characteristics of this virus were studied. Similar observations as noted by Bawden were observed in our experiments, namely, that practically no symptoms are produced by this virus in Datura and tobacco, but that a severe acropetal necrosis develops in Arran Victory and President when infected with D, whereas X develops only a faint mottling. It was not possible to transmit this virus to Bliss Triumph, Green Mountain, and Irish Cobbler. This was to be expected since these varieties are already carrying X, which therefore would protect the plant against infection of any other strain of the same virus.

Necrotic spots were produced, however, in healthy Green Mountain seedling varieties, free from the X virus.

Every attempt to transmit D to seedling 41956, either by leaf mutilation, or by stem grafting, failed, as demonstrated by the impossibility to recover the virus by subsequent inoculations to pepper, indicating that

this variety is resistant to all strains of X virus, which have been tested.

B Virus

Murphy and McKay reported that in their study on comparison of some of the European and American virous diseases of the potato (21), they had considerable difficulty in introducing certain American viruses into healthy President plants. There was found to be throughout the American material a latent virus or viruses, which had a severe necrotic effect on President. They found that this latent virus was present in the "healthy" Green Mountains, as well as in the obviously diseased plants. The writer has made stem grafts of Earliest of All and Bliss Triumph, infected with mild mosaic, crinkle mosaic, and leafrolling mosaic onto healthy Arran Victory and President. In many cases top-necrosis developed on these two varieties. Scions from commercially healthy Green Mountain almost invariably developed similar symptoms, whereas it was produced only occasionally when scions from Burbank, Earliest of All, or Bliss Triumph were used.

These symptoms could not be ascribed to the so-called latent mosaic or X virus, which is universally present in healthy American commercial potatoes, since

this virus produces in these two varieties only a mosaic type of mottling without necrosis.

Grafts from the English variety, Up-to-Date, which according to Bawden, in addition to the X virus carries B, produced typical top-necrosis in President, and Arran Victory. It was considered of interest to determine whether or not the combination of B and X is necessary to produce this disease. Accordingly, double grafts were made of scions from Up-to-Date on healthy scions of X-resistant seedling 41956, which were in turn grafted onto healthy Arran Victory. Typical top-necrosis developed, due to the B virus, since the X virus was filtered out of the complex, as was proven by subsequent inoculation of juice from the infected Arran Victory plants onto Datura and pepper, which failed to show the presence of X. This demonstrated definitely that the B virus alone was responsible for the top-necrosis. Similar double grafts were made, but instead of using Up-to-Date, scions from commercially healthy Green Mountains were made.

Again in these cases top-necrosis developed in Arran Victory, and subsequent sub-inoculations to Datura and pepper demonstrated the absence of the X virus. Since it is known that Katahdin produces a severe top-necrosis when grafted with scions of Green Mountain, the question was raised, whether this symptom is produced by the X or

or by the B virus. Grafts from Arran Victory infected only with B virus and showing current season symptoms of this disease, were made on Katadin. In all cases necrotic circular and rectangular spots developed on the intermediate leaves first, and gradually became evident on every leaf of the plant except the very youngest. Double grafts of Green Mountain on 41956 and Katahdin, as previously described, were also made, and in these cases a top necrosis developed, consisting of a necrotic spotting of the top leaves, and a slight necrosis of the terminal end of the stem. The necrotic spots were larger and not nearly as numerous as those produced by the X virus alone, nor did the top part of the plant die as was true in the case of infection by X.

It appears, therefore, that most of the commercially healthy Green Mountain plants contain, in addition to X, the B virus. Tests made of several plants of Burbank, Earliest of All, and Bliss Triumph varieties grown on the Pacific Coast, with a few exceptions, failed to show the presence of the B virus. The fact that Burbank, Earliest of All, and Bliss Triumph infected with different mosaic viruses produced top necrosis when grafted on Arran Victory and President may be explained by the fact that these plants had become infected by core grafts from mosaic-infected Green Mountain, and by this method the B

virus in addition to the mosaic may have been transmitted from the carrier, Green Mountain.

Grafts on scions from seedling 41956 infected with the B virus alone were made on tomato plants. No symptoms of any kind were discernible, but when scions from these tomatoes were grafted on Arran Victory, typical top necrosis resulted, indicating that tomato is a host of B virus, although failing to show symptoms.

It is not known what effect the B virus has on plants which are merely carriers of it. It does not appear to be as infectious as the X virus since it is not transmissible to potato by leaf mutilation.

Top Necrosis Di Vernon

This virus has been described by Bawden (according to Smith (37)) as C virus. In addition to this the X component is also present.

In the fall of 1934 several plants of the varieties Burbank, Bliss Triumph, and Earliest of All were grafted with scions from infected Di Vernon plants. In nearly all cases current-season symptoms developed which were characterized in these 3 varieties by a severe top necrosis, consisting of a streaking of the stem and petioles and by numerous small circular necrotic spots on the foliage.

The second-generation symptoms of this disease in these varieties, as observed in plants growing under cages in 1935, were manifested by a slight mottling of the foliage without any indications of necrosis. Scions from potato plants showing second-generation symptoms were grafted on Burbank, Earliest of All, and Bliss Triumph. In practically all cases a mottling developed in the grafted plants, and in no case was top necrosis evident. This behavior raised an interesting question. Was the top-necrosis virus destroyed, and another unknown component of the complex responsible for the mottling or had the passage of the virus through plants in which it caused severe necrosis caused the virus to become attenuated? If the virus had become attenuated, it was believed, it would still protect infected plants from developing top necrosis when grafted with scions from Di Vernon. Accordingly 47 plants showing second-generation symptoms were grafted with scions from Di Vernon. Of this number 6 developed top necrosis and the remaining 41 failed to develop any additional symptoms. This indicated protection since a very high percentage of infection was always secured when healthy plants were grafted with this virus. The same observation (namely where an initial top-necrosis, presumably caused by B virus, became a non-necrotic mosaic in the variety

President) have been described by Oortwyn Botjes (6) and Quanjer (27), and have been attributed by the former to attenuation, and by the latter to the presence of 2 viroses, and the elimination of the one producing necrosis.

This virous complex has been transmitted by leaf rubbing to tobacco where the symptoms developed were very similar to those produced by the rugose-mosaic complex, i.e., a severe spot necrosis.

Grafts from infected tobacco plants to potato plants failed to infect the latter. Since the symptoms on tobacco seemed to indicate that one of the components of the complex might be quite similar to the veinbanding mosaic, an effort was made to determine whether plants infected with the Di Vernon complex protects against either the Y or veinbanding virus. Accordingly 5 potato plants showing second-generation symptoms of this virous complex were inoculated with the Y virus and each one of them became infected. Ten infected potato plants were inoculated with the veinbanding virus, and each of these also showed the presence of this virus. These results would indicate that the Y-virus group is not related to any of the viroses found in the Di Vernon complex.

Double grafts of scions of Di vernon on 41956,

and then on President, developed typical top necrosis on the latter. Since the seedling 41956 filters out the X virus, and since the absence of this virus in the infected President variety was indicated by subsequent inoculations to pepper, it was proven that the X-virus component is not necessary to produce top-necrosis symptoms.

Scions from a Green Mountain plant showing current season symptoms of top necrosis were grafted on President and on healthy Green Mountain seedlings. Circular necrotic spots developed in the intermediate leaves, but not in the young top foliage. This seemed to indicate that acro-necrosis develops only when a carrier of C virus, like Di Vernon, is grafted on a susceptible potato plant, whereas a scion from a plant showing top necrosis due to current season infection will produce only acropetal necrosis. Tubers from plants having top necrosis as current symptoms of C-virus infection when subsequently grafted on susceptible plants, give rise to plants which show only a mottling and which have lost the power to produce top necrosis.

Although the symptoms in tobacco produced by this virous complex suggests the presence of the Y-like virus, all other evidence indicates that none of the components

of the virous complex belong to the Y-virus group. Whereas the Y-like viruses are readily transmitted to potato by leaf mutilation, all attempts to transmit to this host the virous components in the extracted juice of Di Vernon plants failed to produce any symptoms. The Y-virus group produce acropetal necrosis on potatoes, whereas this particular virous complex causes a definite acro-necrosis as current season symptoms in the same varieties. It is believed that the component causing top necrosis in this virous complex is different from any of the potato viroses found in America.

Tuber Blotch

The virus causing this disease was first described in 1933 by Loughnane and Clinch (19) who isolated it from Glasnevin stock harboring interveinal mosaic, which according to these authors, is caused by a combination of tuber blotch and X virus.

This virus has been transmitted by leaf mutilation to a number of potato varieties, namely, Green Mountain, Irish Cobbler, Bliss' Triumph, Katahdin, and some miscellaneous seedlings. In some of these seedlings necrotic blotches developed on the intermediate leaves. Katahdin also developed severe necrosis of the leaf blade due to infection with the tuber-blotch virus. In

seedling 41956, a faint Aucuba-like chlorosis developed and similar symptoms were observed in Green Mountain, and Bliss Triumph. In Irish Cobbler a foliar necrosis instead of chlorotic blotches developed.

Tubers from infected Bliss Triumph plants showed an internal patchy like necrosis, but the data on tuber symptoms of all of these varieties is not as yet complete. Symptoms in the tubers do not develop until 2 or 3 months after harvesting.

In Nicotiana glutinosa yellow aucuba-like symptoms were produced quite similar to those found in White Burley tobacco, consisting of irregular yellow patches on the leaf. In Nicotiana sylvestris distinct light necrotic areas developed in the tissue between the veins of the leaf blade giving the plant a rusty appearance. The symptoms in pepper plants consisted of longitudinal streaking of the stem and necrotic spots on the top leaves, which latter finally dried down and hung on the stem by means of dried up petioles. Eventually every leaf of the plant dried down and dropped.

Ten President plants infected with this virus were inoculated with Canada-Streak virus (which will be discussed later). The plants were kept under observation for $2\frac{1}{2}$ months, but failed to show any additional symptoms. At the end of that period, one

leaf from each of the ten plants was taken, the juice was extracted and inoculated into 10 plants each of potato and Nicotiana sylvestris. Only tuber blotch symptoms developed. Five healthy President plants inoculated with Canada-Streak virus developed severe foliar necrosis 3 weeks after inoculation.

Property studies of this virus show that it can be diluted 1-500 and still cause infection, its thermal death point is from 63° to 65° F., and it can exist in vitro for about 96 hours.

Pseudo Net Necrosis

This disease was first described by Quanjer, Thung and Elze (39) in 1929. They found the symptoms consisting of necrotic spots in the storage parenchyma next to the external and internal phloem of the tubers only. They recorded that pseudo-net necrosis developed during storage and that its development was accelerated by a rise in temperature.

The writer has transmitted this virus by leaf rubbing to a number of potato varieties, such as Green Mountain seedlings, some numbered seedlings of miscellaneous varieties, Bliss Triumph, and Katahdin. In most of the seedlings necrotic blotches developed on the intermediate leaves. Small yellow blotches were

evident on the leaves of infected Bliss Triumph. In Katahdin a very pronounced necrosis of the tissues between the veins of the leaf blade developed, and some necrosis was found on the midribs and smaller veins. The intermediate leaves turned yellow and eventually dropped. The study of tuber symptoms of this disease has not as yet been completed.

In Nicotiana sylvestris small circular Aucuba-like spots developed on the leaves, but no indications of necrosis were evident. Small yellow spots also appeared on infected Burley tobacco plants. Nicotiana glutinosa developed on irregular yellowish blotchy type of symptoms. The effect on pepper was quite similar to that produced by tuber blotch and also caused death of the plant about 20 days after inoculation.

President plants infected with this virus were inoculated with Canada-Streak virus. These plants were kept under observation for 2½ months, but failed to show any additional symptoms. One leaf was taken from each of the ten inoculated plants, and the extracted juice was inoculated into 10 plants each of potato and Nicotiana sylvestris. As in the case where tuber-blotch infected plants were inoculated with Canada streak, Pseudo net-necrosis symptoms only developed.

The property studies of this virus show it to be

very similar to that causing tuber blotch. It is still infective when diluted 1-500, its thermal death point is 63° to 65° F., and it can exist *in vitro* for about 96 hours.

Aucuba Mosaic

Quanjer (25) was the first to describe the Aucuba mosaic disease of potato plants and so named it on account of its resemblance to the natural mottling of *Aucuba japonica*. This disease is distinct from the one having the same name in tomato, and which is caused by a virus closely related to the common tobacco mosaic virus. In 1926 Atanasoff (2) stated that net necrosis was a tuber symptom of Aucuba mosaic, in which the parenchymatous tissues of the tuber become necrotic but the vascular tissue is not involved. In 1929, Elze and Quanjer (12) came to the conclusion that Atanasoff had been dealing with a mixture of Aucuba mosaic and pseudo-net necrosis and that he was incorrect in regarding the latter as a symptom of Aucuba mosaic.

The symptoms of this disease are uniform in most of the different American and European potato varieties tested and consist of small, round, bright yellow spots about 4 mm. in diameter, which may coalesce to form large yellow patches. In the European variety, British Queen,

foliar necrosis and a wilting of leaves develops in addition to a pronounced yellow mottling. This has also been reported by Clinch et al (9). These authors found that the presence of A virus caused an exaggeration of the mottle. We did not find this true in the variety, Green Mountain and seedling 41956. These two varieties infected with A virus were inoculated with Aucuba mosaic, but no more difference in the intensity of the chlorotic spots of the leaves was found than in those of the healthy plants of the same variety inoculated with Aucuba mosaic. Clinch et al (9) found tuber necrosis in the parenchymatous cells of both cortex and pith, and visible externally as irregularly shaped brown patches. They found tuber necrosis in seven of the fourteen varieties examined, although in some it was very mild. Our studies of tuber symptoms have not been completed.

This virus has also been studied in tobacco, and a number of other solanaceous plants. Quanjer (26) stated that tobacco was a symptomless carrier of this virus and Clinch et al (9) also state that tobacco is readily inoculable, but shows no symptoms. In our studies we found irregular yellow blotches on the upper half of the leaves.

Symptoms somewhat similar to those found in tobacco, but more uniformly-distributed over the entire leaf were found in Nicotiana glutinosa. In N. sylvestris

a few scattered semi-dried up spots develop on the leaf blade. Definite necrotic spots were evident in the top leaves of infected pepper plants. These finally dry down and under relatively high temperature conditions, 75° F. and above, the plant dies within about 20 days after inoculation.

No symptoms could be detected following inoculation of Petunia, but no return inoculations were made to potato to determine whether this plant is a masked carrier.

Property studies of this virus show that it can be diluted 1-500 and still cause infection, its thermal death point is 65° to 68° C., and it can exist *in vitro* for 96 hours.

Canada Streak

In the spring of 1934 a tuber of the variety, Irish Daisy, infected with an unknown virus was received from Mr. Putman of the University of Toronto. At that time the disease was tentatively designated as Canada streak. It was found to be readily transmitted to different potato varieties by juice transfer which generally resulted in 100% infection. Symptoms developed within three weeks and varied with different varieties, although the intensity of the symptoms varied considerably at times within the same variety. A blotchy mottling of the lower leaves resembling somewhat Aucuba-like symptoms has been

in the seedling 41956. In other cases stem necrosis, a burning of the veins and petioles in addition to Aucuba-like symptoms have been observed in any one variety. When juice from chlorotic plants was transferred to Bliss Triumph, considerable leaf necrosis developed similar to that which occurred when they were inoculated with juice from necrotic plants. In the early stages, second-generation symptoms of Earliest of All infected with Canada streak were manifested by a rugosity of the leaves which had a tendency to roll downward. The veins of the lower leaves were necrotic. When the plants grew larger necrotic spots appeared on the foliage resembling "early blight" infection, except that concentric rings were absent. In addition some yellow blotches were also evident. In some cases only a chlorotic mottling and a few necrotic spots appeared on the leaves.

The symptoms in Green Mountain corresponded in general to those found in Earliest of All. In Irish Cobbler the lower leaves were fairly well covered with necrotic areas but no yellow spots were found on them. Some yellowing was evident in the top leaves and the lower leaves finally dropped. Considerable necrosis was found in the stem and this extended into the cortex and pith. In Chippewa necrotic dried-up areas were found on the intermediate leaves, but practically no Aucuba-like

symptoms were evident. In President necrotic spots were found on the lower and intermediate leaves, and typical Aucuba-like symptoms on the top leaves. In Epicure, necrotic blotches and streak symptoms were practically absent. The lower leaves were chlorotic, with just a little of the green interspersed. Infected Arran Victory plants showed considerable of the Aucuba-like symptoms in addition to the necrotic spots on the lower and intermediate leaves.

It was found that in practically all cases an internal necrosis consisting of brown patches developed inside the tubers of infected plants, but these symptoms generally did not become evident until about two months after harvesting.

White Burley tobacco plants have been inoculated with this virus, and these developed irregular white blotches on the upper half of the leaves. When young pepper plants were inoculated with Canada streak, leaves developed necrotic blotches, stems became necrotic and within 20 days after inoculation the plants were dead. This was not true of older infected plants which developed necrotic leaves and leafdrop, but the plants were not killed.

In Nicotiana glutinosa brownish dried-up areas appeared on the top leaves. These soon disappeared and a typical Aucuba type of mottling developed. In

Nicotiana sylvestris dried-up spots about 2 mm. in diameter developed on most of the leaves in addition to small circular yellow spots.

Experiments were carried out in 1935 to determine whether this virus could be transmitted by aphids. About 20 aphids taken from caged potato plants infected with Canada streak were transferred to each of 77 sprouted potato seed pieces on which they were permitted to feed for 6 days. Forty-seven seed pieces were colonized with Myzus circumflexus, Buckl., 18 with Myzus pelargonii, Kalt., and 12 with Macrosiphum solanifolii (Ashm.). After the aphids had fed on the seed pieces for 6 days, they were fumigated and planted in the field. The plants were kept under observation until maturity, but in no case were any disease symptoms observed.

The yellow blotches on the foliage, which in addition to necrosis, were generally evident, suggested that there might be a relationship between this disease and Aucuba mosaic. Through the courtesy of Dr. K. Starr Chester, these two viruses causing the above mentioned diseases were subjected to a serological test. In a letter dated May 29, 1937, Dr. Chester stated: "The close relationship of Canada streak to potato Aucuba mosaic has been repeatedly confirmed." This evidence, however, does

not necessarily exclude the fact that the disease is not caused by a virous complex of two components, one of which may be responsible for the Aucuba-mosaic symptoms, and the other for the necrotic spots on the foliage and the internal brown spots of the tubers.

A number of experiments were designed to demonstrate whether Canada streak is due to a single virus or to more than one component. It was believed that a combination of Aucuba mosaic and tuber blotch would be the most likely components, since the latter causes necrotic spots in foliage of some potato varieties and an internal brown spot in tubers. Accordingly, series of inoculations of viruses of Canada streak alone, Aucuba mosaic alone, tuber blotch alone, and equal parts of juice extracted from Aucuba-mosaic-infected and from tuber-blotch infected plants were made into young potato plants of different varieties, i.e., British Queen, Green Mountain, Bliss Triumph, and Irish Cobbler, and the symptoms observed.

In the variety British Queen, Canada streak, Aucuba mosaic and tuber blotch caused a foliar necrosis and wilting, while Aucuba mosaic and Canada streak produced also bright chlorotic patches on the leaves. In Irish Cobbler and Green Mountain the combination of Aucuba mosaic and tuber blotch, caused, in addition to Aucuba-mosaic symptoms, a slight foliar necrosis due to

the tuber blotch, but the symptoms were quite different from those caused by Canada streak. In Bliss Triumph the combination of tuber blotch and Aucuba mosaic failed to produce any necrosis, whereas foliar necrosis in this variety is quite pronounced when it is infected with Canada streak.

In transmission studies of tuber blotch to other solanaceous plants, it was found that ordinarily a smaller percentage of infection took place than when Canada-streak virus was used as the source of infection. In the several hundred inoculations which have been made with the last named virus, into several different host plants, the Canada-streak symptoms were always observed. This was true when property studies of this virus were carried out and at times only a small percentage of infection also was secured. If this disease is due to a virous complex consisting of more than one component, it is believed that occasionally one of the components would fail to be transmitted and this fact would be evidenced by the type of symptoms produced.

All the available evidence supports the fact that Canada streak is due to a single virus which is a strain of Aucuba mosaic which also produces necrosis.

The properties of this virus are quite similar to those of Aucuba mosaic. It can be diluted 1-500 and still

cause infection, its thermal inactivation point is 65° to 68° C., and it can exist *in vitro* for 96 hours. (Table 2)

The Aucuba Virous Group

Clinch et al (9) in their grouping of potato viroses propose to establish a new group, namely viroses of the F type, in which should be included pseudo-net necrosis, tuber blotch, and Aucuba mosaic. On the basis of performance and property studies they have come to the conclusion that tuber blotch and pseudo-net necrosis are probably identical and that the Aucuba virus is a related but distinct form. As a result of the writer's experiments he is in complete accord with this proposed grouping, and believes that tuber blotch and pseudo-net necrosis are identical. Since the term "pseudo-net necrosis" was first designated by Quanjer and his co-workers, this name should be retained on account of priority and the term "tuber blotch" discarded.

Canada streak has proven to be a strain of Aucuba mosaic and therefore belongs in this group. It is proposed to designate the virus causing this disease also as "G" and refer to it as a strain of Aucuba mosaic.

Calico

This disease was first described by Hungerford (14)

in 1920. It is characterized in most potato varieties by the occurrence of large irregular yellow to cream colored spots on the leaves. The spots may be sparse, or numerous and well distributed over the plant. This disease has been studied only during the fall of 1937 and the spring of 1938, primarily to determine the relationship if any between this virus and those belonging to the Aucuba mosaic.

In Nicotiana sylvestris a very pronounced yellow mottling develops on the leaves, and the yellowish patches have a slight tendency to dry up, giving the plant in addition to the mottling a somewhat rusty appearance. In N. glutinosa irregular shaped yellowish blotches develop over the entire surface of the leaf.

In pepper very definite calico symptoms develop, very similar to those found in potato, and no indications of necrosis were evident. Since the symptoms in this host were so different from those caused by the viroses belonging to the Aucuba-mosaic group, which produce a severe necrosis generally resulting in death of the plant, it was considered of interest to determine whether or not Calico-infected pepper plants would protect against infection of viroses belonging to this group. Accordingly, 4 series each consisting of 10 Calico-infected pepper plants were inoculated with Aucuba mosaic, Canada streak,

tuber blotch, and pseudo-net necrosis, respectively. Within two weeks, necrotic lesions on the leaves, and necrotic streaking of the petioles developed in every plant inoculated. This demonstrated definitely that no protection against infection of any of these viroses was afforded by Calico infection of pepper. Additional experiments including serological and property studies should be conducted but on the basis of the results secured to date no relationship between Calico and the viroses of the Aucuba-mosaic group has been demonstrated.

DISCUSSION

An attempt has been made to determine the components of the different viroses affecting potatoes in Europe and in this country. The latent mosaic of healthy potatoes, or the X virus, is universally present in all of the older commercial varieties grown in the United States, so that all virous diseases affecting those varieties are due to combinations at least of 2 or more components. The development of seedling 41956 by the U. S. Department of Agriculture, found to be immune from the X virus, has been of considerable aid in isolating the components of virous complexes. A number of the European virous diseases were also found to be due to complexes including X, but in some cases were due only to one component.

These different components individually and the

virous complexes have been studied in several different American and European potato varieties and also in other solanaceous host plants. In addition, the longevity of the virus outside the host, the effect of dilution of the virus on infectivity and its reaction to various pH concentrations have been determined in some cases. Serological determinations and protective inoculation studies have also been employed to determine the relationship between different viruses.

On the basis of symptoms and general behavior it is believed that enough evidence has been secured to determine that crinkle, mild mosaic and crinkle mosaic are so similar, that although not identical, they may be considered as closely related strains of the same virus. All three of these viroses are composed of two components. Crinkle contains in addition to X the component designated by Murphy as A. It is proposed that the virous component in mild mosaic and crinkle mosaic, in addition to X, be designated as A. The A derived from either one of the 3 viruses mentioned produces only a faint mottling in the varieties, President, Majestic, and a seedling of Green Mountain. When these plants are later inoculated with the X virus, the mottling and crinkling of the leaves is considerably intensified. It was of special interest to observe that A virus derived from crinkle as well as from

mild mosaic produced typical top-necrosis without any mottling when infected scions were grafted on Up-to-Date or British Queen.

Leafrolling mosaic appeared to be different from any of the known viroses occurring in potatoes in Europe. It has been suggested by Murphy that this virus may have affinities with para-crinkle. These two diseases have been studied in comparison in several different American and European potato varieties, but no similarity of symptoms were found in any of these. Whereas, leafrolling mosaic manifested itself in most of the varieties by a soft upward rolling of the leaves in addition to a diffused mottling, para crinkle, on the other hand, failed to produce a rolling and developed large mosaic-like blotches on the leaves of most varieties. Leafrolling mosaic can be transmitted by juice transfer while all attempts to transmit para crinkle by this method failed.

The absence or presence of the X virus in the leafrolling-mosaic complex did not appear to effect any significant difference in the development of symptoms in the varieties, President and Arran Victory. It is proposed to designate as "E" the component causing leafrolling mosaic.

The veinbanding virus in combination with X causes the disease known as rugose mosaic. This virus

has been studied in comparison with Kenneth Smith's Y virus and the stipple streak from Holland. The symptoms caused by these three viroses in different potato varieties and other solanaceous plants vary in intensity but are quite similar in general appearance. Of these three viruses the stipple streak and veinbanding appear to be more similar to each other than the Y virus is to either one of them. The last named one is considerably more severe in its attack on plants. It was found that when Green Mountain and Bliss Triumph plants infected with rugose mosaic were inoculated with the Y virus no additional symptoms developed, although the effect of Y on healthy plants of the same varieties was much more severe than that of the veinbanding virus. The Y virus also failed to produce additional symptoms on Zealand Blue potato plants infected with stipple streak, nor was it possible to recover the Y virus from such inoculated plants by making return inoculations from them on 20 tobacco plants, since the typical stipple-streak type of symptoms, instead of the Y type, developed. Serological studies by Chester showed that these three viroses are serologically indistinguishable. Since all evidence indicates that they are closely related strains, it is proposed to designate all three of them as Y.

Different strains of X virus have been found in some of the European and American potato varieties. The

intensity of symptoms of such complexes causing crinkle and mild mosaic varied somewhat, depending upon the strain of X present in the complex. This virus has been successfully transmitted from potato to Amaranthus rectoflexus, on which it produced necrotic spots on the leaves. It has been readily recovered from this host as was shown by return inoculations to Datura. The D virus described by Bawden (4), is, as was intimated by him, an aberrant strain of X. On varieties like President and Arran Victory it produced, instead of a mottling as is typical in other tested strains of X, a severe foliar necrosis which shows up again in plants from tubers from infected plants. On Datura and tobacco it develops very faint symptoms and protects against infection of other strains of X. It is believed that this virus should also be designated as X instead of D. Seedling 41956 was found to be immune from all strains of X virus tested.

The B virus, which is universally present in combination with X in the European variety Up-to-Date which serves as a masked carrier of both of these viroses, was secured in biologically pure form, by making double grafts of scions of Up-to-Date on to seedling 41956 and Arran Victory. The B virus alone produced typical top necrosis. Tomato was found to be susceptible to this

virus, but failed to develop any symptoms. Scions of infected tomato plants on Arran Victory produced top necrosis. It was demonstrated that this virous components was practically always found in commercially healthy Green Mountain and it has also been isolated from this variety by the double graft method, using seedling 41956 as an intermediate graft. Several plants of Bliss Triumph, Irish Cobbler, and Burbank from the Pacific Coast were tested for the presence of B, but with the exception of 2 Burbank plants, all results were negative.

Virus C which, according to Salaman (32) is universally present in the variety Di Vernon, was readily transmitted by grafting to all of the American varieties tested and produced severe top necrosis as current-season symptoms, but second-generation symptoms consisted of normal sized plants, showing a distinct, but faint mottling. Grafts of scions from such plants onto different susceptible varieties produced only a mottling instead of top necrosis. When scions of Di Vernon were grafted on potato plants manifesting second-generation symptoms, of 41 plants grafted only 6 developed top necrosis, apparently showing protection since a very high percentage of infection was always secured when healthy plants were grafted.

The C component was secured free from the X, by

grafting the complex onto seedling 41956, and by making double grafts using 41956 as an intermediate, on healthy President and Majestic. Typical top necrosis developed, showing that the X virus is not necessary to produce these symptoms. The C component alone produced a veinclearing on tobacco plants, and the C and X components together caused typical spot necrosis on this host, indistinguishable in appearance from the symptoms produced by rugose mosaic. Inoculation studies failed to show any protection of the C virus against infection of Y.

Clinch, et al (9) found that pseudo-net necrosis and tuber blotch are identical, and the writer's experiments confirm this. They state that these two viruses produce an inconspicuous yellow mottle of the lower leaves or no symptoms in the lower leaves of twenty-five varieties tried. In our work it was found that in some varieties, like Green Mountain and Bliss Triumph, and especially Irish Cobbler, considerable foliar necrosis developed in addition to a yellow mottle. A foliar necrosis and yellow mottling was also found in Nicotiana sylvestris infected with either one of these two viruses. The experiments have not been carried far enough to study tuber symptoms produced by these viruses, although a necrosis has been observed in infected Bliss Triumph potatoes.

Clinch et al (9) also found that Aucuba mosaic and tuber blotch of potato produced identical symptoms in Solanum nodiflorum, and Capsicum annuum; This also has been confirmed and it was found that similar symptoms are also produced in Nicotiana glutinosa and N. tobaccum, but there was a slight difference on N. sylvestris. In potato varieties Aucuba mosaic produced considerably more mottling than caused by the other two viruses. The writer is in accord with their proposal to designate the tuber-blotch virus as "F" and the virus of Aucuba mosaic, as "G". The tuber-blotch virus, however, is held as a synonym of pseudo-net necrosis which may be designated as "F".

A new undescribed virus received from Canada and tentatively designated as Canada streak was found to be a strain of Aucuba mosaic. In most potato varieties it produced severe foliar necrosis in addition to a yellow mottle or variegation on the lower and middle leaves. In some instances longitudinal streaking of stem and petiole of some varieties was observed. Serological studies proved it to be indistinguishable from Aucuba mosaic, and protective studies showed it to be related to tuber blotch and pseudo-net necrosis. It is proposed to designate this virus also as virus G, and refer to it as a strain of Aucuba-mosaic virus.

Calico was found to produce some of the same general

Type of symptoms in potato plants as those caused by viroses belonging to the Aucuba-mosaic group, i.e., yellow to cream-colored spots on the leaves, although the blotches are much more irregular in shape than those produced by Aucuba mosaic. The greatest contrast in symptoms was produced in pepper in which Calico produced large yellow spots, whereas the other viruses caused severe foliar necrosis. Since Calico-infected pepper plants failed to protect against infection of any of the viroses of the Aucuba-mosaic group, it is believed that no relationship exists between this group and the calico virus.

SUMMARY

The chief symptoms, as found in different American and European potato varieties and some other solanaceous plants, are described for mild mosaic, crinkle mosaic, crinkle, leaf-rolling mosaic, para-crinkle, veinbanding, Y virus, stipple streak, X virus, top necrosis B virus, top necrosis C virus, tuber blotch, pseudo-net necrosis, Aucuba mosaic, Canada streak, and Calico.

The relationship existing between different viroses has been determined on the basis of (1) similarity of symptoms in different host plants, (2) by protective inoculation, (3) serological similarities, and (4) by

studying the relation of certain physical properties of viroses (such as longevity *in vitro*, dilutions, and the thermal inactivation point) to infectivity.

Mild mosaic, crinkle mosaic, and crinkle were found to be so similar in many respects that although they are not identical they are so closely related that the component in addition to X found in the virous complex causing each of the three diseases, is designated as "A".

Leafrolling mosaic was found to be distinct from para-crinkle. The virus in the complex, in addition to X, is designated as "E".

Veinbanding, Y virus, and stipple streak vary somewhat in the severity of symptoms produced in different hosts, but the general type of symptoms are similar. Serological and property studies prove that they are closely related strains of the same virus, and all three are designated as "Y".

No relationship was found between the veinbanding and cucumber-mosaic virus on the basis of inoculations in potato and tobacco. None of the Y viroses protected against infection of cucumber mosaic in tobacco.

Amaranthus rectoflexus was found to be a host of X virus. D virus proved to be an aberrant strain of X. Seedling 41956 was found to be immune from all strains of X virus tested.

B virus produces top necrosis in the varieties Arran Victory and President. Green Mountain was found to carry this virus in addition to X. It was not found in the varieties Bliss Triumph, Burbank and Earliest of All.

C virus causes top necrosis in all of the American potato varieties tested. The tuber-perpetuated symptoms in these varieties consist of a mottling. Grafts of scions from such plants to healthy potatoes produce a mottling instead of a top necrosis.

Pseudo-net necrosis and tuber blotch were found to be identical, and this virus is designated as "F".

Canada streak is a strain of Aucuba mosaic producing necrotic spots in the parenchyma of the tubers in every variety tested. This virus, the same as the one causing Aucuba mosaic, is designated as "G".

The Aucuba-mosaic group of viroses includes pseudo-net necrosis, Aucuba mosaic and Canada streak.

Calicooon the basis of incomplete studies, does not seem to be related to the viroses of the Aucuba-mosaic group.

Table 1. A summary of comparison of the properties of the Y-group viruses.

Viruses derived from	Thermal inactivation point (°C.)*	Number infected	Tolerance to dilution	Number infected	Longevity in vitro at 15° C.* hours	Number infected	Resistance to pH, using disodium phosphate-citric acid buffer, after 24 hours*	Number infected
Y virus from England	50	10•/10••	1-10	10/10		10/10	2.2	10/0
			1-100	10/8	24		3.8	10/0
	54	10/7	1-200	10/8			4.2	10/1
			1-300	10/6	48	10/9	4.7	10/5
	56	10/2	1-400	10/8			5.	10/5
			1-500	10/5	72	10/3	5.6	10/9
	57	10/0	1-600	10/2			6.	10/8
			1-700	10/2	96	10/0	7.	10/6
	59	10/0	1-800	10/0			8.5	10/4
			1-900	10/0			1-10	10/10
	61	10/0	1-1000	10/1			H_2O	
	Untreated control	10/10						
Stipple streak from the Nether-lands	50	10/10	1-10	10/10	24	10/9	2.2	10/0
			1-100	10/10			3.8	10/0
	54	10/1	1-200	10/9	48	10/8	4.2	10/0
	56	10/0	1-300	10/6			4.7	10/2
	57	10/0	1-400	10/10	72	10/2	5.	10/3
	59	10/0	1-500	10/8			5.6	10/8
	61	10/0	1-600	10/8	96	10/0	6.	10/6
	Untreated control	10/9	1-700	10/8			7.	10/6
			1-800	10/6			8.5	10/2
			1-1000	10/4			1-10	10/9
				10/2			H_2O	
Vein-banding virus from North America	50	10/8	1-10	10/10	24	10/9	2.2	10/0
			1-100	10/6			3.8	10/0
	54	10/2	1-200	10/4	48	10/8	4.2	10/1
			1-300	10/2			4.7	10/3
	56	10/4	1-400	10/6	72	10/2	5.	10/5
		10/0	1-500	10/0			5.6	10/9
	57	10/0	1-600	10/4			6.	10/6
			1-700	10/4			7.	10/7
	59	10/0	1-800	10/0			8.5	10/6
	61		1-900	10/2			1-10	10/10
	Untreated control	10/10	1-1000	10/0			H_2O	

• Upper figure, number of plants inoculated.
•• Lower figure, number infected.
* Virus extract diluted 1-10.

Table 2. A summary of comparison of the properties of the Aucuba-mosaic group of viruses

Viruses derived from	Thermal inactivation point (°C.)*	Number infected	Tolerance to dilution	Number infected	Longevity in vitro at 15° C.*	Number infected	Resistance to pH, using disodium-phosphate citric acid buffer, after 24 hours*	Number infected
					hours			
	60	10•/10••	1-10	10/8	24	10/9	2.2	10/0
Aucuba	62	10/10	1-100	10/6	48	10/8	3.8	10/0
	65	10/7	1-500	10/2	72	10/5	4.2	10/2
	68	10/0	1-1000	10/0	96	10/1	4.7	10/6
	Untreated	10/10					6.	10/6
							8.5	10/2
	60	10/8	1-10	10/10	24	10/10	2.2	10/0
	62	10/10	1-100	10/10	48	10/8	3.8	10/0
Canada	65	10/6	1-500	10/4	72	10/6	4.2	10/3
streak	68	10/0	1-1000	10/0	96	10/5	4.7	10/3
	Untreated	10/10					6.	10/5
							8.5	10/1
	60	10/6	1-10	10/8	24	10/8	2.2	10/0
	62	10/7	1-100	10/5	48	10/7	3.8	10/0
Pseudo-	65	10/0	1-500	10/0	72	10/4	4.2	10/1
net	68	10/0	1-1000	10/0	96	10/1	4.7	10/3
necrosis	Untreated	10/6					6.	10/4
							8.5	10/0
	60	10/7	1-10	10/7	24	10/8	2.2	10/0
	62	10/5	1-100	10/6	48	10/6	3.8	10/1
Tuber	65	10/0	1-500	10/3	72	10/3	4.2	10/0
blotch	68	10/0	1-1000	10/0	96	10/0	4.7	10/3
	Untreated	10/7		10/0			6.	10/4
							8.5	10/1

• Upper figure, number of plants inoculated.
•• Lower figure, number infected.
* Virous extract diluted 1-10.

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Plate 1

Fig. 1. Leaflet from Green Mountain potato infected with mild mosaic.

Fig. 2. Leaflet from Green Mountain infected with crinkle.

Fig. 3. Leaflet from Majestic infected with A virus derived from mild mosaic.

Fig. 4. Leaflet from Earliest-of-All infected with mild mosaic.

Fig. 1

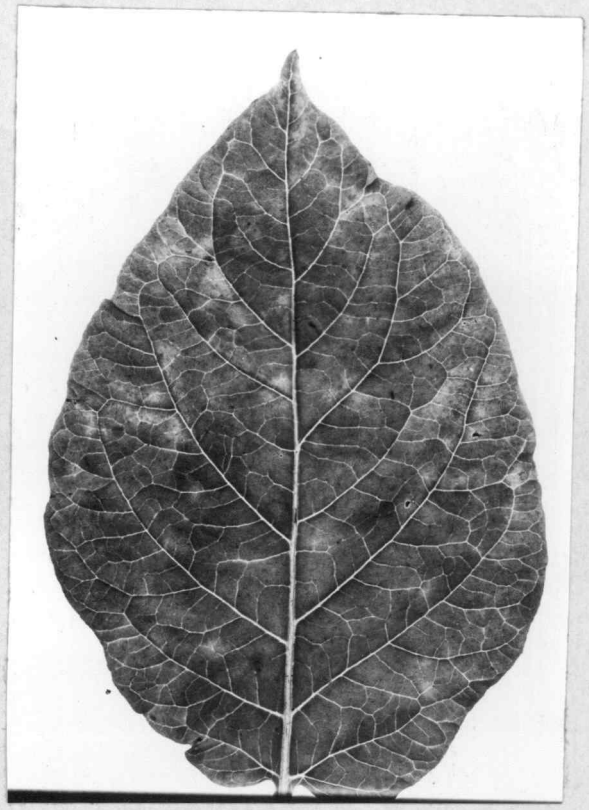


Fig. 2

Fig. 3

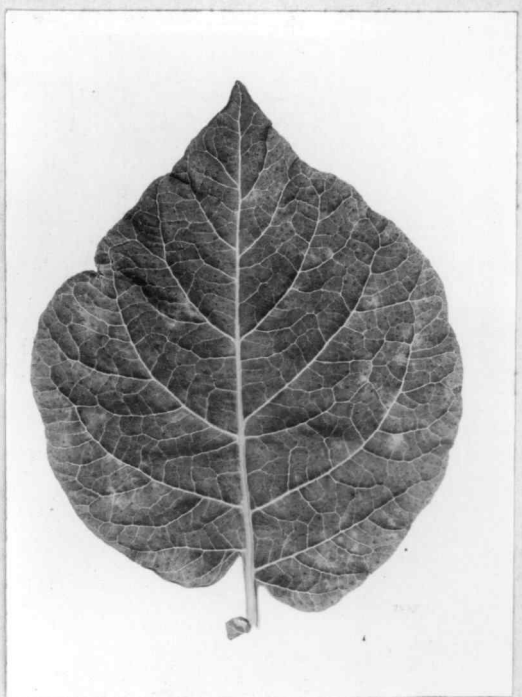


Fig. 4

Plate 1

Plate 2

Fig. 1. Leaflets from three different plants of seedling, variety 41956, infected, respectively, with crinkle, mild mosaic, and crinkle mosaic. Since this seedling is immune from X, this component has been removed from the virous complexes. A=crinkle-X,B= mild mosaic-X, C= crinkle mosaic-X.

Fig. 2. Leaflet from President infected with crinkle.

Fig. 3. Leaflet from President infected with mild mosaic.

Fig. 1

Fig. 2

Fig. 3

Plate 2

Plate 3

Fig. 1. Leaflet of Bliss Triumph infected with crinkle.

Fig. 2. Bliss Triumph plant infected with crinkle.

Fig. 1

Fig. 2

Plate 3

Plate 4

Fig. 1. British Queen plant showing current season infection of mild mosaic due to the grafting of a scion from seedling 41956 infected with A virus. Typical top necrosis, free from mottling developed. The infected plant was free from X virus.

Fig. 2. Current season infection of mild mosaic on Up-to-Date, secured by grafting onto it a scion from seedling 41956 infected with A virus. Note the top necrosis in this variety.

Fig. 1

Fig. 2

Plate 4

Plate 5

Fig. 1. "A" virus from mild mosaic in tobacco leaf, secured by inoculating juice from an infected 41956 seedling into tobacco plant. Symptoms are faint, but the virus was recovered by making return inoculations to potato.

Fig. 2. "A" virus from mild mosaic in tomato leaflet, secured by grafting a scion from an infected 41956 seedling onto tomato plant.

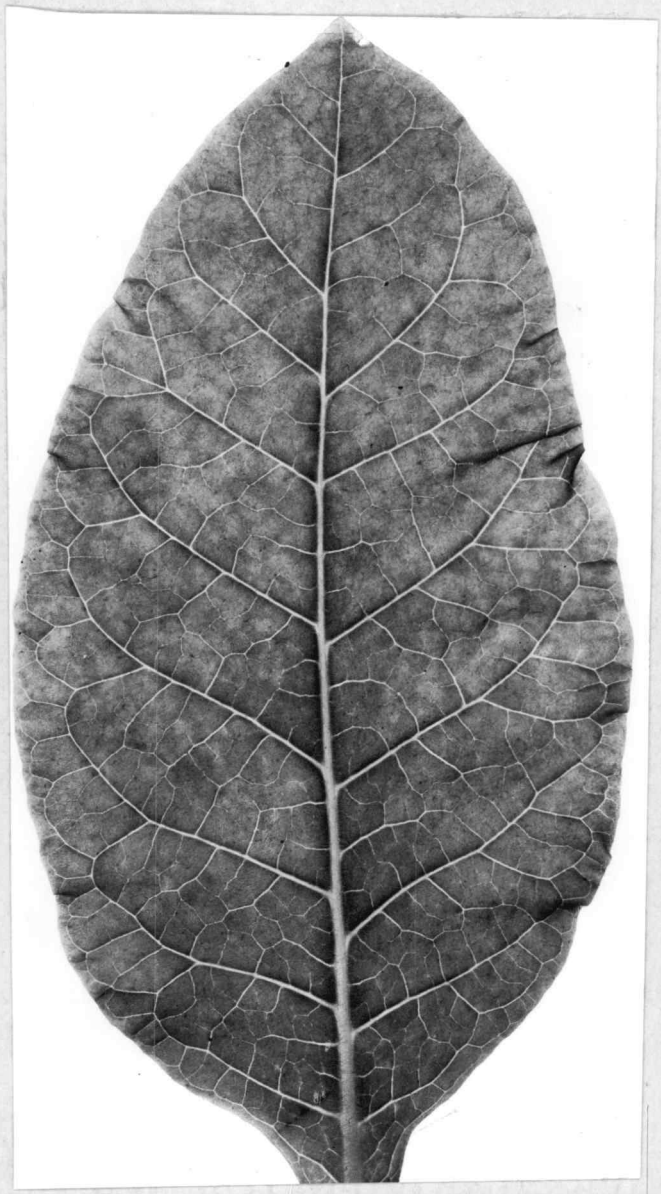


Fig. 1

Fig. 2

Plate 5

Plate 6

Fig. 1. "A" virus from crinkle mosaic in tobacco leaf, resulting from inoculating juice from an infected 41956 seedling into tobacco plant.

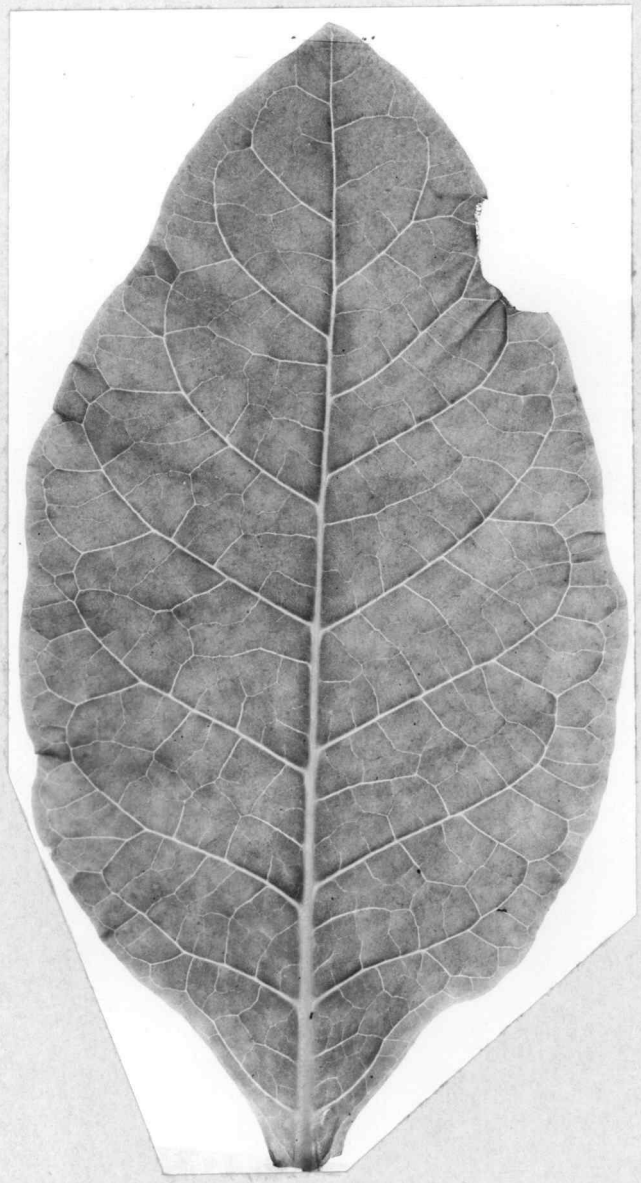


Fig. 1

Plate 6

Plate 7

Fig. 1. "A" virus from crinkle in tobacco leaf, due to inoculating the plant with juice from seedling 41956 infected with this virus.

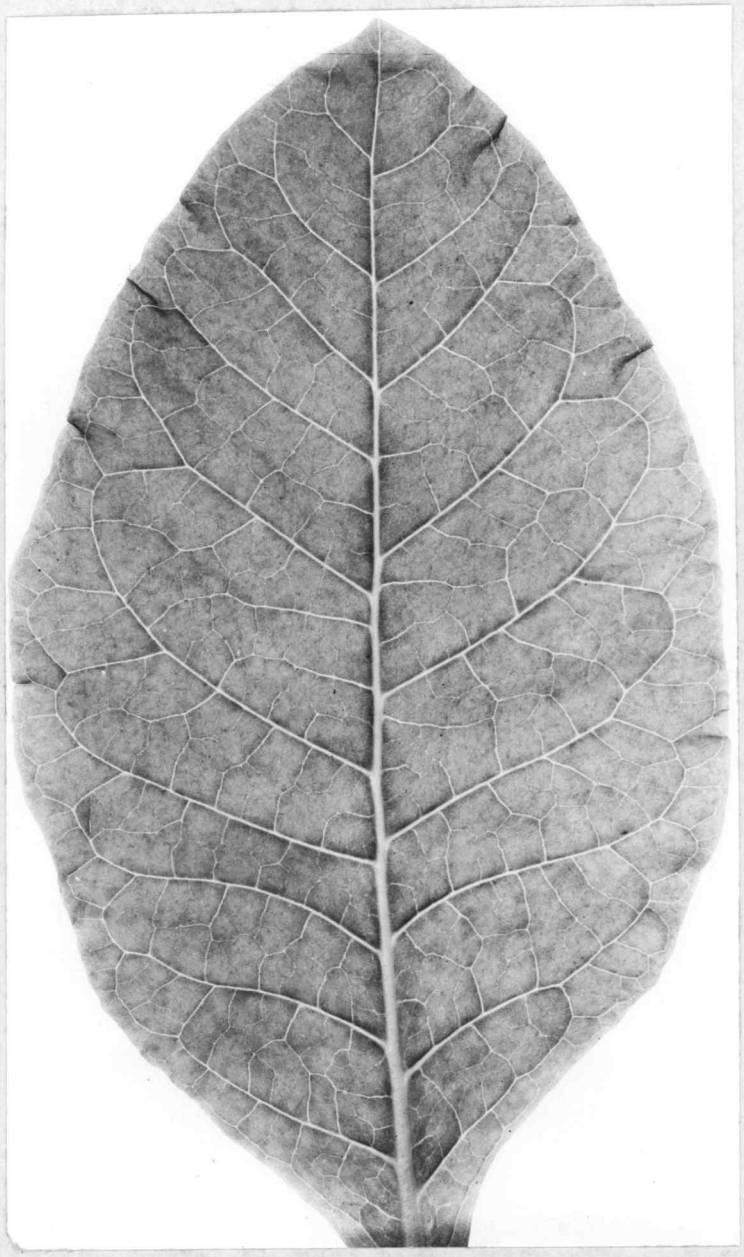


Plate 7

Plate 8

Fig. 1. "A" virus from crinkle in Nicotiana sylvestris due to inoculating the plant with juice extracted from an infected 41956 seedling. Notice the clearing of the veins, and the blotchy type of mottling.

Fig. 2. "A" virus from mild mosaic in N. sylvestris, resulting from infection of the mild-mosaic virus from which the latent-virus component had been removed by passing through seedling 41956. Notice the similarity in symptoms caused by "A" virus derived from the European crinkle and the one derived from American mild mosaic.

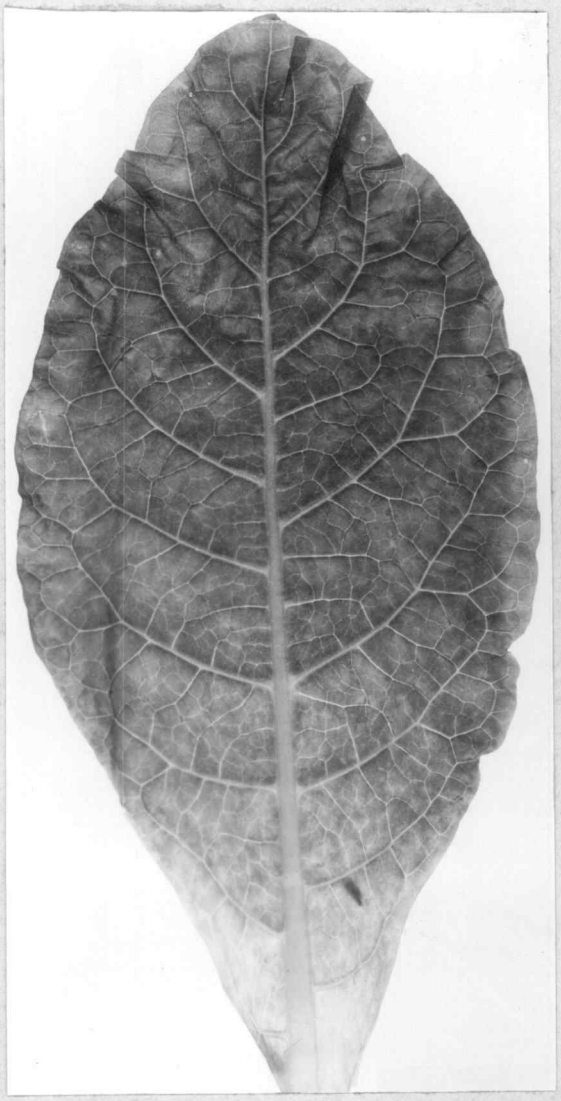


Fig. 1

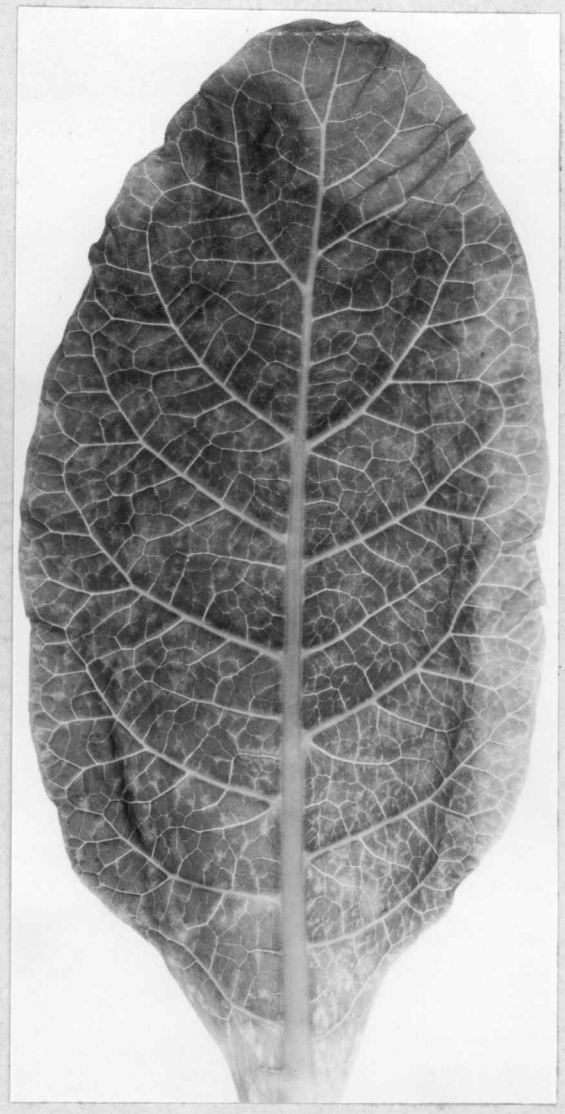


Fig. 2

Plate 8

Plate 9

Fig. 1. A - Healthy plant of seedling 41956.

B - Leafrolling mosaic on seedling 41956, due to grafting a scion from a leaf-rolling-mosaic-infected Bliss Triumph containing "X" onto this plant. The "X" virus was removed from the complex and the remaining virus causing the soft rolling of the leaves and an interveinal type of mottling is designated as virus "E".

Fig. 1

Plate 9

Plate 10 and 10 A

Fig. 1. Leaf from Arran Victory plant infected with virus "E".

Fig. 2. Leaf from Arran Victory plant infected with leafrolling mosaic due to the virous complex, E and X. Notice that mottling is more pronounced than in the leaf infected only with virus "E".

Fig. 1

Plate 10.

Fig. 2

Plate 10 A

Plate 11

Fig. 1. Para crinkle in tomato leaves caused by grafting a scion from an infected Arran Victory plant onto tomato. Return grafts from such tomato plants to healthy Arran Victory reproduced the disease.

Fig. 2. Para-crinkle symptoms on leaflet from an infected Burbank plant which was growing under cages in the field. Notice the pin-point-like necrotic spots.

Fig. 3. Para-crinkle symptoms on a leaflet from an infected Earliest of All plant growing in the greenhouse. A chlorotic type of mottling is evident.

Fig. 1

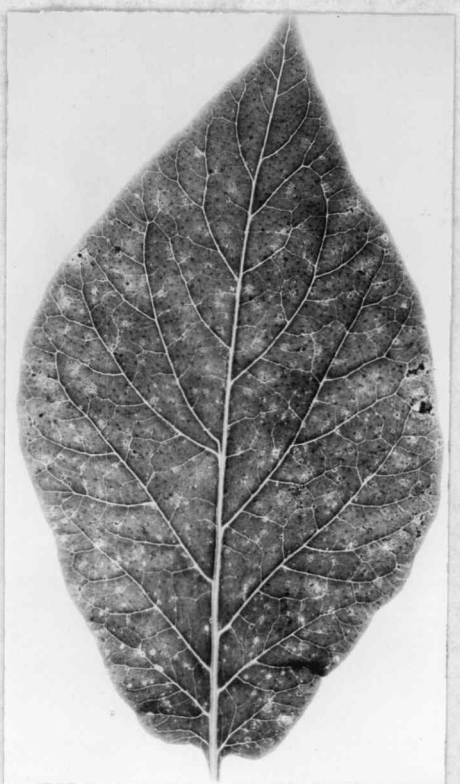


Fig. 2

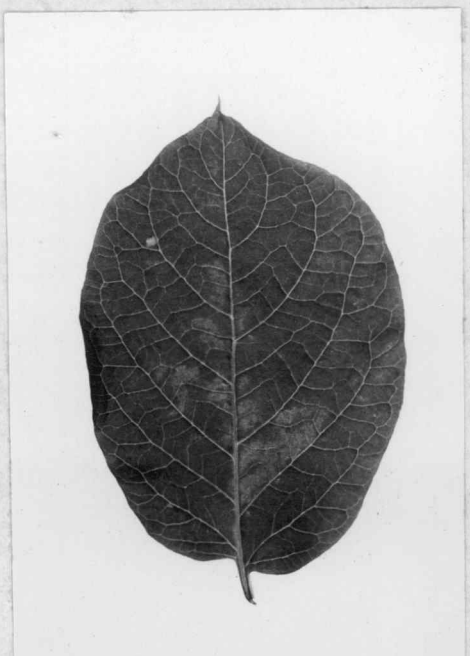


Fig. 3

Plate 11

Plate 12

Fig. 1. Leaflets from a para-crinkle-infected Arran Victory plant. The diseased tuber from which this plant developed came directly from England and was used as the source of infection in the study of this disease. No indications of the presence of X virus were detected in the plant.

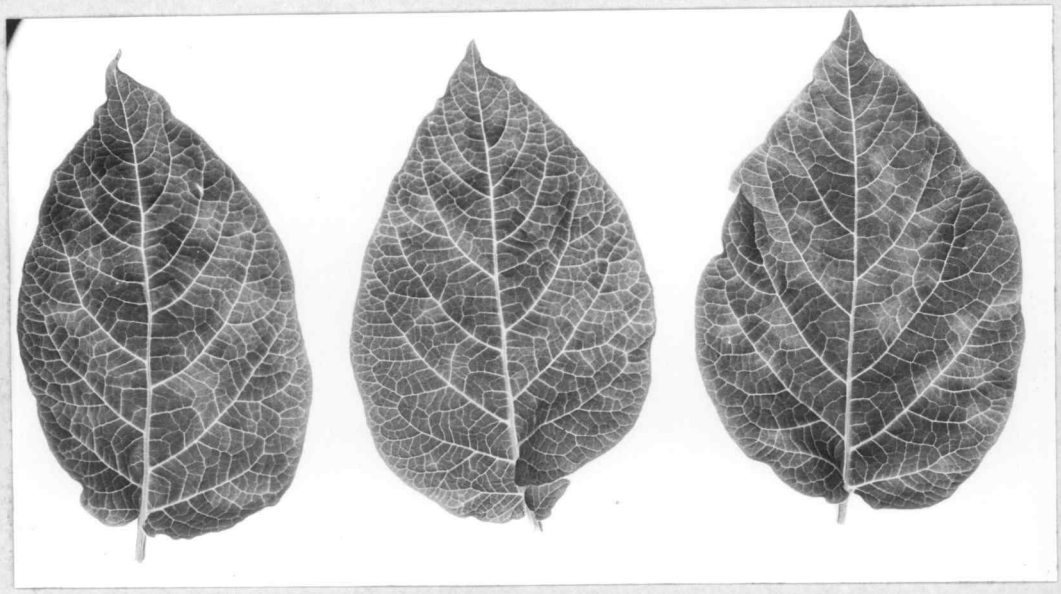


Fig. 1

Plate 12

Plate 13

Fig. 1. Tobacco leaf infected with veinbanding mosaic.

Fig. 2. Tobacco leaf infected with Y virus. Notice that the symptoms are of the same general type, but Y causes a more pronounced clearing of the veins than the veinbanding mosaic.

Fig. 3. Pepper leaf infected with veinbanding mosaic.

Fig. 4. Pepper leaf infected with the Y virus.

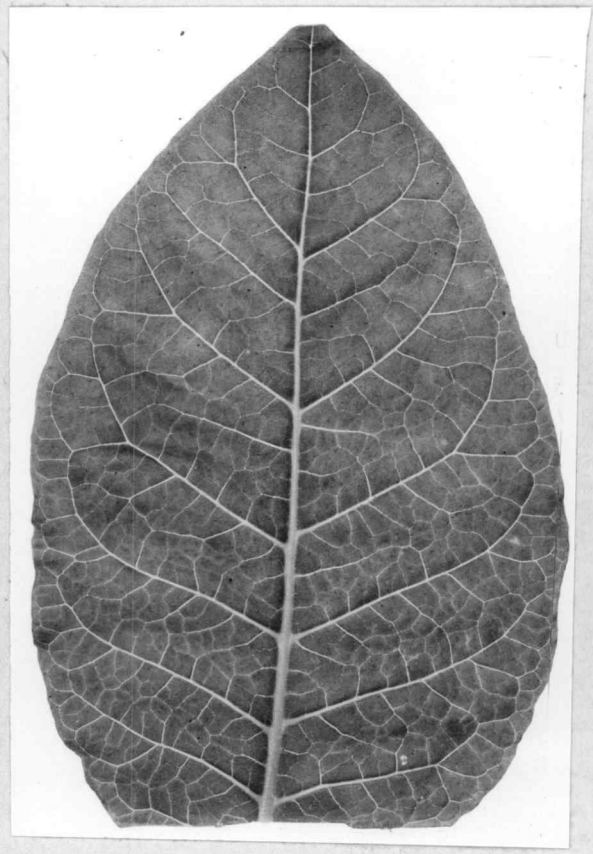


Fig. 1

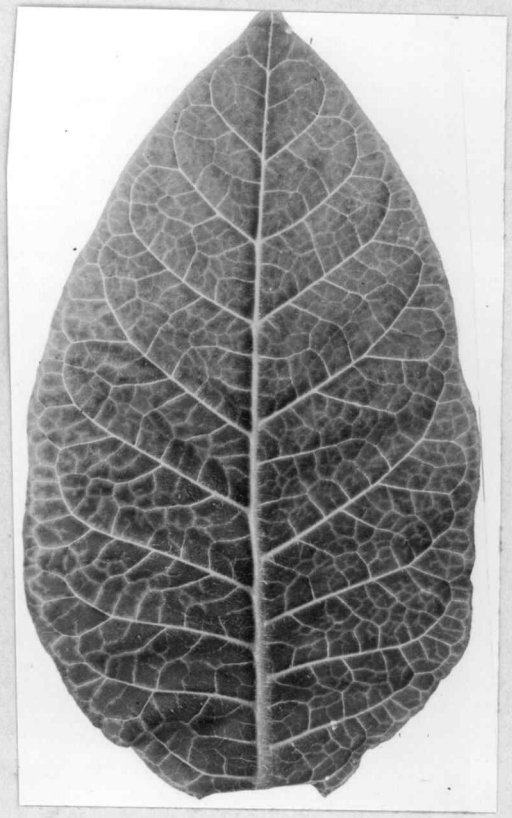


Fig. 2

Fig. 3

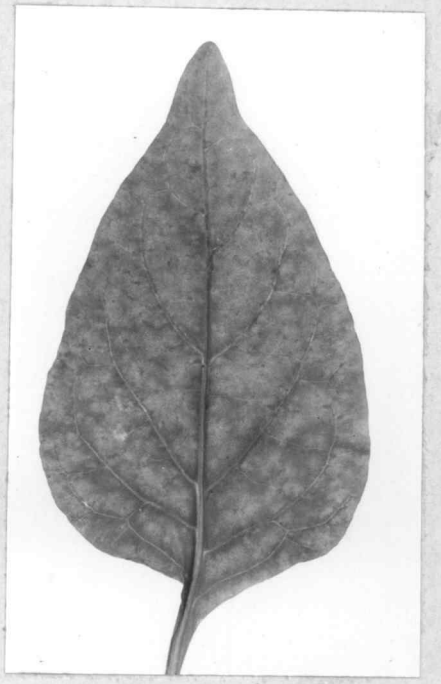


Fig. 4

Plate 13

Plate 14

Fig. 1. A - Burbank potato plant showing tuber-perpetuated symptoms of veinbanding mosaic. Since Burbank also contains the X virus, the disease caused by the virous complex is known as rugose mosaic.

B - Burbank potato plant showing tuber-perpetuated symptoms of Y virus. The tubers yielding this plant and the one shown in figure 1-A were planted the same day. Note that the effect of the Y virus is much more severe than that caused by the veinbanding virus.

Fig. 2. A - White Rose potato plant showing tuber-perpetuated symptoms of Y virus.

B - White Rose potato plant showing tuber-perpetuated symptoms of the veinbanding virus.

A B

Fig. 1

A B

Fig. 2

Plate 15

Fig. 1 A - President plant free from the X virus showing tuber-perpetuated symptoms of the Y virus. Notice the leaf dropping.

B - President plant showing tuber-perpetuated symptoms of the veinbanding virus.

Fig. 2 A - Bliss Triumph plant showing tuber-perpetuated symptoms of the Y virus.

B - Bliss Triumph plant infected with the veinbanding virus.

A B

Fig. 1

A B

Fig. 2

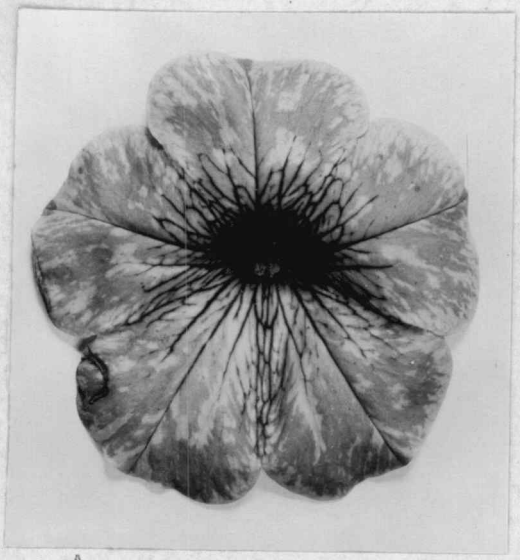
Plate 15

Plate 16

Fig. 1 A - Petunia flower showing a distinct mottling in the petals due to infection of the veinbanding mosaic.

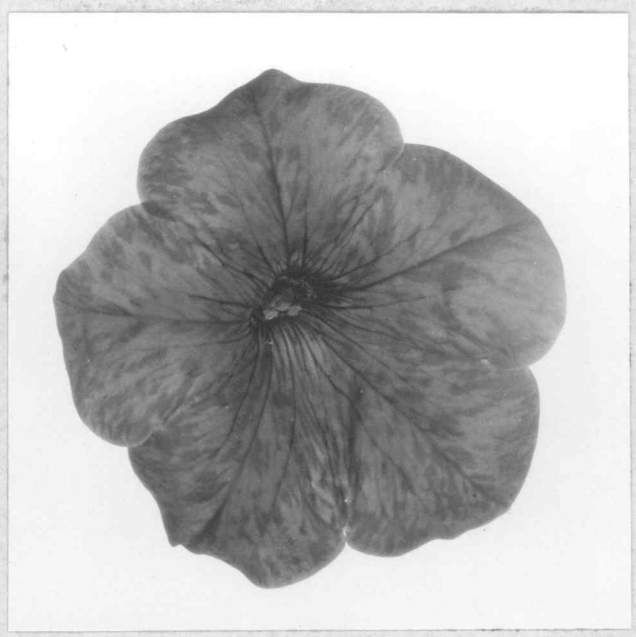
B - Flower from a petunia plant infected with stipple-streak virus. Notice the similarity in symptoms caused by this and the veinbanding virus.

Fig. 2 Leaves from Nicotiana sylvestris infected with A = Y virus, B = veinbanding, C = stipple streak.



A

Fig. 1



B Fig. 1

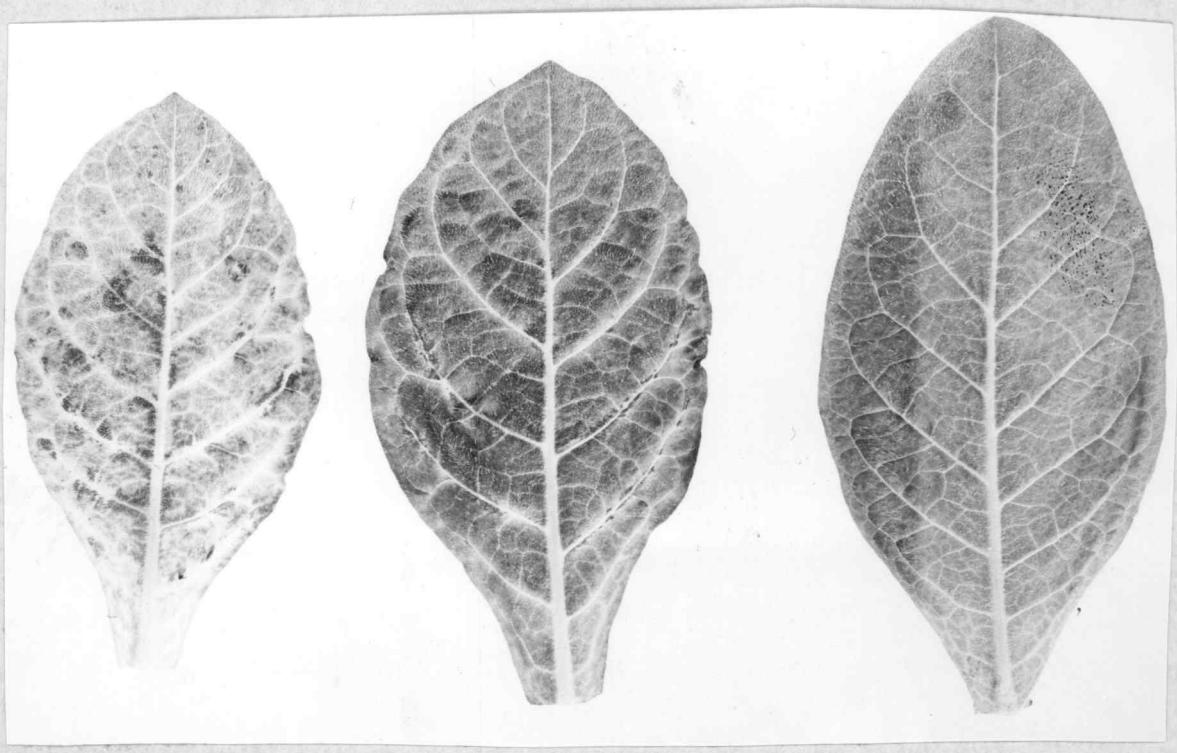


Fig. 2

Plate 16

Plate 17

Fig. 1 Tobacco leaf from plant infected with X virus.

Fig. 2 Tomato leaflet showing a mottling due to infection of the X virus.

Fig. 3 Arran Victory plant showing tuber-perpetuated symptoms of D virus (an aberrant strain of X virus). Notice the necrotic blotches on the leaves.

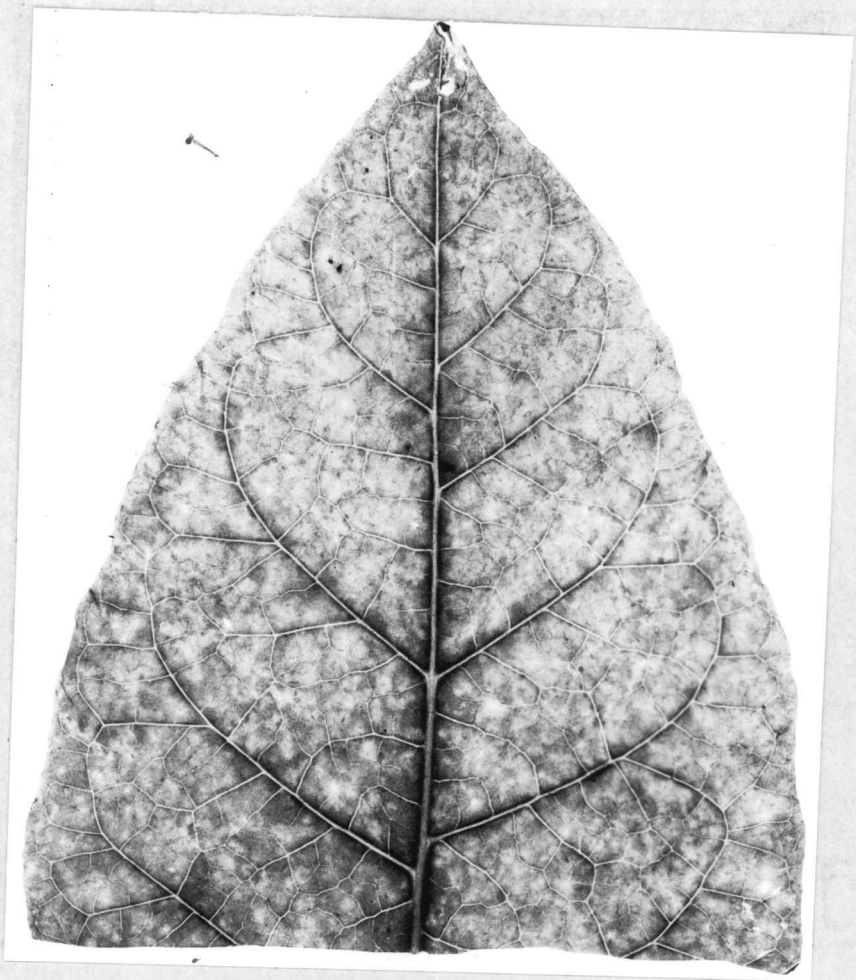


Fig. 1

Plate 17

Fig. 2

Fig. 3

Plate 17

Plate 18

Fig. 1. A - Jimson weed (*Datura stramonium*) infected with X virus. Notice the distinct mottling on every leaf of the plant.

B - Control, healthy plant.

Fig. 2. Leaflets from pigweed, *Amaranthus rectoflexus*, necrotic blotches due to infection of X virus.

Fig. 3. Leaflet from *Solanum villosum* infected with X virus.

A B

Fig. 1

Fig. 2

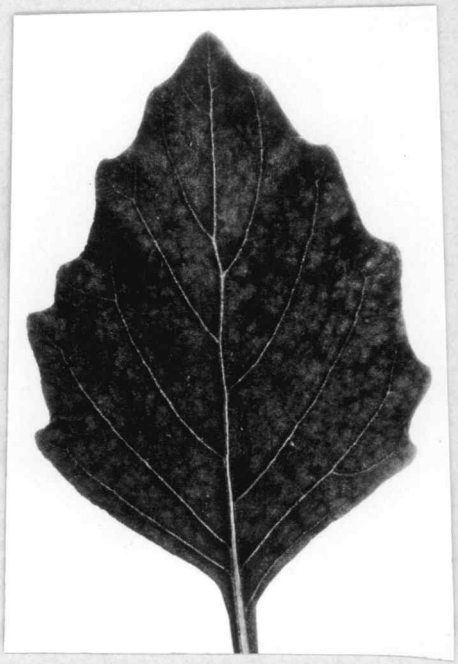


Fig. 3

Plate 18

Plate 19

Fig. 1 *Amaranthus rectoflexus* infected with X virus, due to inoculating the plant with juice from a potato plant containing this virus. The presence of X was demonstrated by making return inoculations to Jimson weed in which the characteristic X symptoms developed.

Fig. 1

Plate 19

Plate 20

Fig. 1. Arran Victory plant showing top necrosis due to infection of B virus alone. A scion from Up-to-Date carrying both X and B virus was grafted onto X-resistant seedling 41956. The X virus was removed by this seedling variety, and a scion from it containing only B virus was grafted onto a healthy tomato plant, which failed to develop symptoms. When a scion from this plant was grafted onto Arran Victory typical B-virus symptoms, namely top necrosis, developed. Subsequent inoculations from this plant to Jimson weed and pepper failed to show the presence of the X virus.

Fig. 2. Leaflet from Arran Victory infected with top necrosis showing the type of necrotic spotting.

Fig. 1

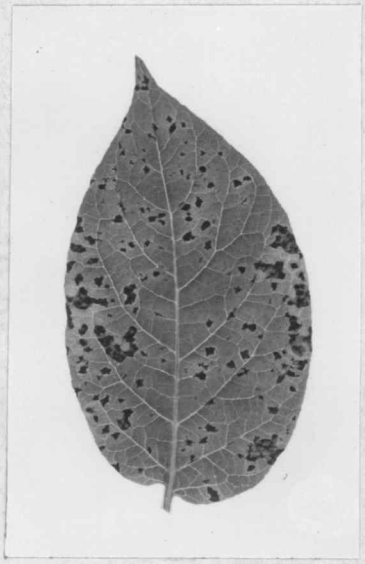


Fig. 2

Plate 20

Plate 21

Fig. 1. Arran Victory plant showing the initial symptoms of top necrosis due to B virus. Infection was secured by double grafting a scion from a Green Mountain (carrying both the X and B virus), on seedling 41956 and Arran Victory. The B virus was transmitted and the X eliminated.

Fig. 2. Advanced stages of top necrosis due to infection of B virus from Green Mountain in Arran Victory.

Fig. 1

Plate 21

Fig. 2

Plate 21

Plate 22

Fig. 1 A - Katahdin plant showing infection due to the B virus alone. Notice that only necrotic lesions are present in the top leaves, but the stem does not show any symptoms. Photo taken 20 days after graft was made.

B - Katahdin plant showing top necrosis due to infection of the X virus alone. Notice that the top part of the stem is killed. Photo taken 19 days after the graft was made.

A B

Fig. 1

Plate 22

Plate 23

Fig. 1. Earliest of All plant showing top necrosis, a current symptom due to infection of C virus, secured by grafting a scion from an infected Di Vernon plant on a healthy Earliest of All.

Fig. 2. Earliest of All plant showing tuber-perpetuated symptoms of C virus. Notice that only a chlorotic mottling is evident.

Fig. 1

Plate 23

Fig. 2

Plate 23

Plate 24

Fig. 1. Leaflet from a Burbank potato plant showing necrotic spotting due to current season infection of C virus.

Fig. 2. Leaflet from a Bliss Triumph potato plant infected with C virus.

Fig. 3. Necrotic spotting on leaflet from a C-virus-infected Earliest of All plant.

Fig. 4. A leaflet from a Majestic plant infected with the C virus alone free from the X.

Fig. 1

Fig. 2

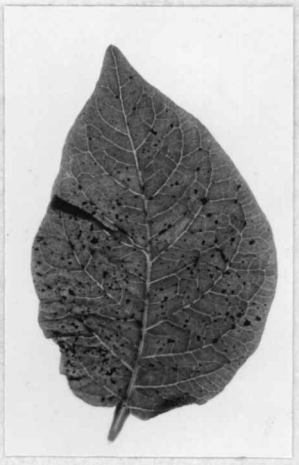


Fig. 3

Fig. 4

Plate 24

Plate 25

Fig. 1. Tuber-perpetuated symptoms of C virus in Bliss Triumph found only in progeny from a plant which failed to develop current season symptoms when grafted with a scion from an infected Di Vernon plant the preceding season.

Fig. 2. Leaflet from Bliss Triumph showing tuber-perpetuated symptoms of C virus. Leaflet was secured from a plant having shown these symptoms for three generations.

Fig. 3. Bliss Triumph plant, which showed mottling due to second generation infection of C virus was grafted with a scion from a Di Vernon plant containing the C virus. Current season symptoms consisting of top necrosis developed again. This was found to take place in 6 of the 47 plants which were thus grafted, showing that in most cases the virus, carried over in the tubers, afforded protection against renewed infection of the C virus.

Fig. 1

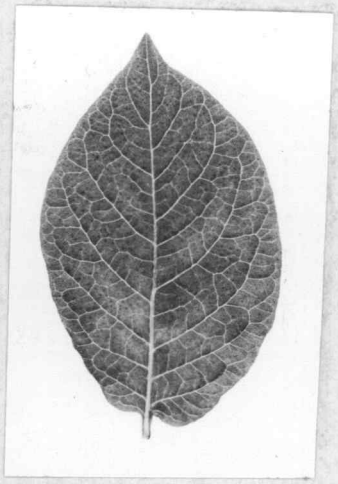


Fig. 2

Fig. 3

Plate 25

Plate 26

Fig. 1. Tobacco plants showing the early symptoms of spot necrosis due to infection of a combination of C and X viruses. Photo taken 13 days after inoculation.

Fig. 2. Tobacco leaf showing the advanced symptoms of spot necrosis due to infection of a combination of C and X viruses. Photo taken 25 days after inoculation.

Fig. 3. Section of a tobacco leaf showing symptoms due to infection of C virus alone, free from X virus. Photo taken 25 days after inoculations.

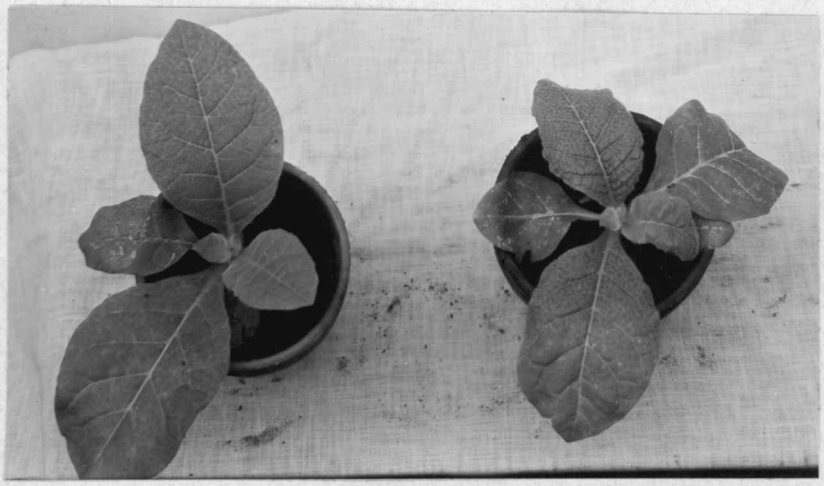


Fig. 1

Fig. 2

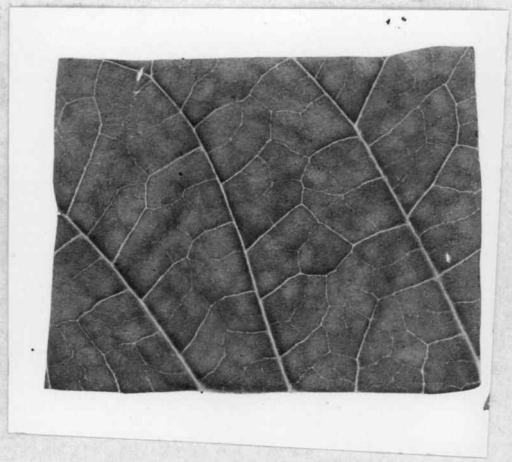


Fig. 3

Plate 26

Plate 27

Fig. 1. Leaflet from Irish Cobbler showing necrotic areas due to infection of the tuber-blotch virus.

Fig. 2. Leaflets from a Green Mountain seedling infected with tuber blotch showing a slight yellow mottling and a necrotic spotting of the leaf.

Fig. 3. Leaflet from Irish Cobbler infected with pseudo-net necrosis. Notice the necrotic blotches on the leaf.

Fig. 4. Leaflet from President infected with pseudo-net necrosis. Necrotic spotting is absent, but a yellow blotchy type of mottling is very noticeable.

Fig. 1

Fig. 2

Fig. 3

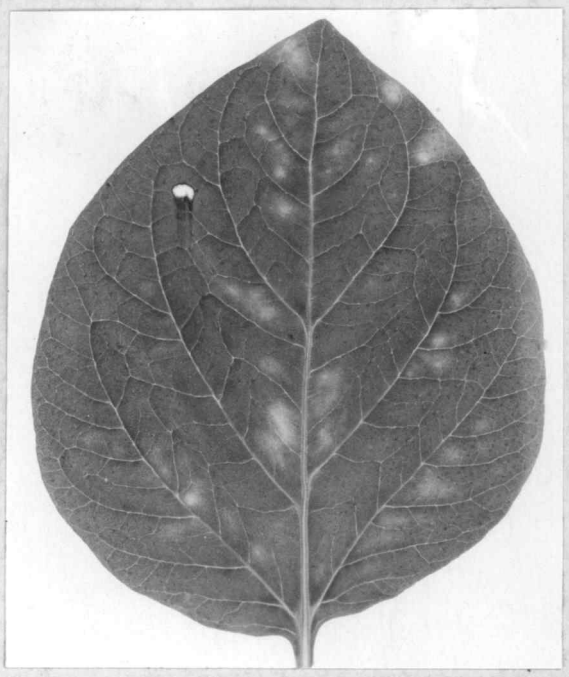


Fig. 4

Plate 27

Plate 28

Fig. 1. Tobacco leaf showing symptoms due to infection with tuber-blotch virus alone. An irregular blotchy type of mottling is evident.

Fig. 2. A leaf from Nicotiana glutinosa plant infected with the tuber-blotch virus. The blotches are somewhat smaller and brighter in color than those found in tobacco.

Fig. 3. A leaf from Nicotiana sylvestris infected with tuber blotch alone. Both a mottling and a faint necrosis is evident.

Fig. 1

Fig. 3

Fig. 2

Plate 28

Plate 29

Fig. 1. Leaf from tobacco plant infected with the pseudo-net-necrosis virus alone.

Fig. 2. Leaf from Nicotiana glutinosa showing symptoms due to infection of pseudo-net necrosis.

Fig. 3. Leaf from Nicotiana sylvestris showing Aucuba type of mottling due to infection of the pseudo-net-necrosis virus.

Fig. 1

Fig. 3

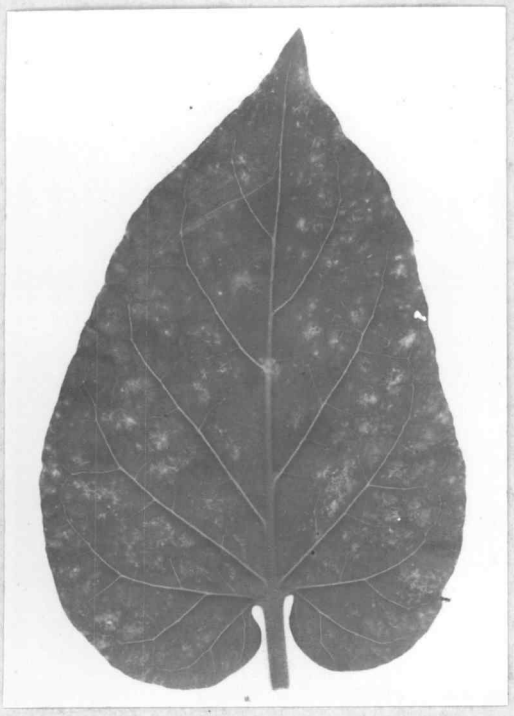


Fig. 2

Plate 29

Plate 30

Fig. 1. Leaf from tobacco plant showing a blotchy type of mottling due to infection of the Aucuba-mosaic virus, free from the X.

Fig. 2. Leaf from an Aucuba-mosaic-infected Nicotiana glutinosa plant. Notice the similarity in symptoms of tuber blotch, pseudo-net necrosis, and Aucuba mosaic on this host.

Fig. 1

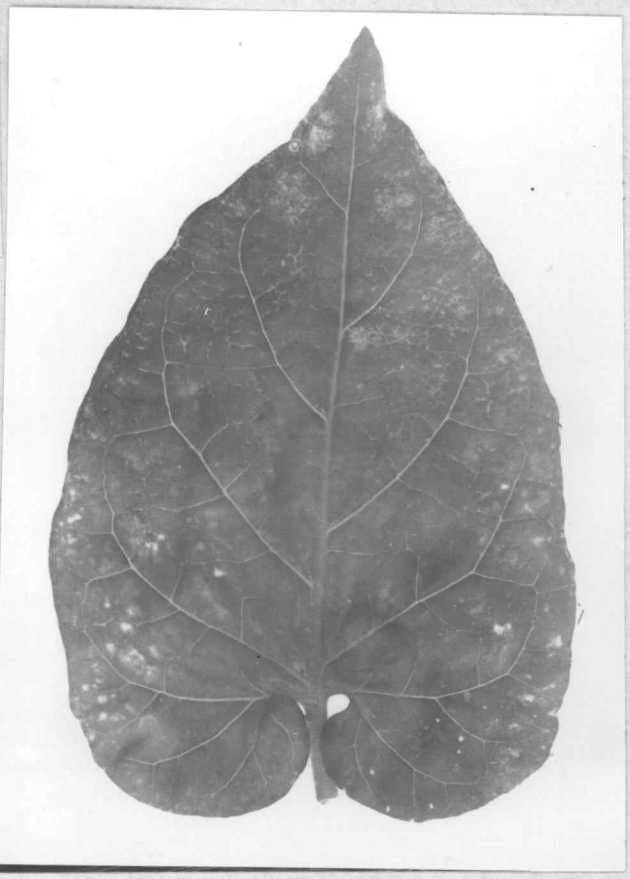


Fig. 2

Plate 30

Plate 31

Fig. 1. Pseudo-net-necrosis symptoms on *Solanum nodiflorum*.

Fig. 2. Leaf from *Solanum nodiflorum* showing symptoms of Aucuba mosaic.

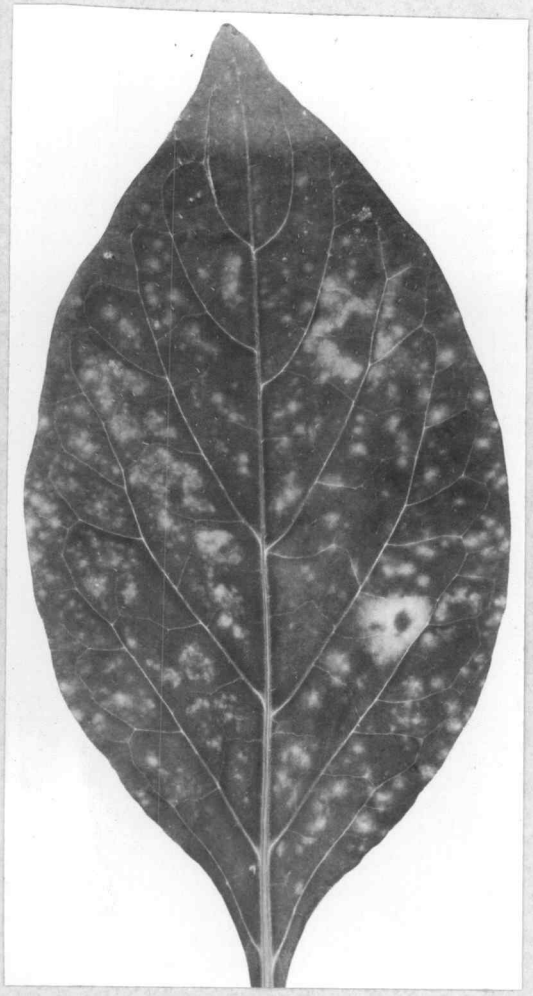


Fig. 1

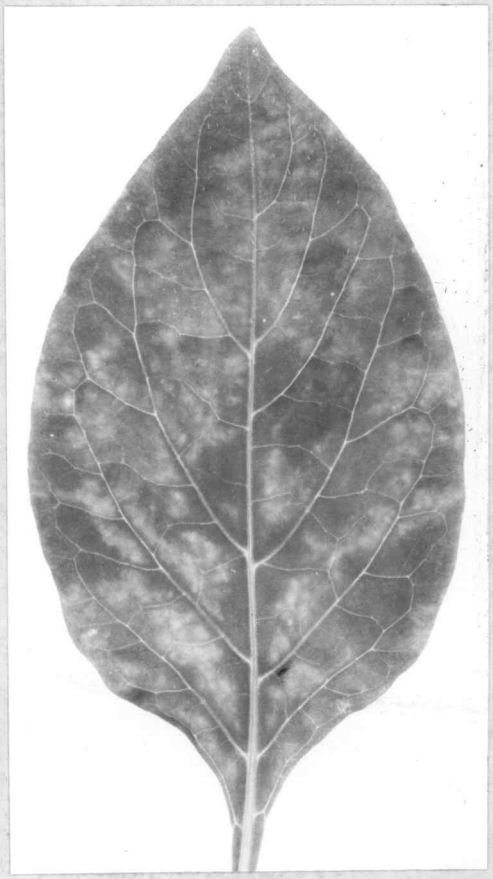


Fig. 2

Plate 31

Plate 32

Fig. 1. Tobacco leaves showing symptoms due to infection of Canada-streak virus, free from the X virus.

Fig. 2. Tobacco leaf showing considerable necrosis due to infection of Canada streak and X virus.

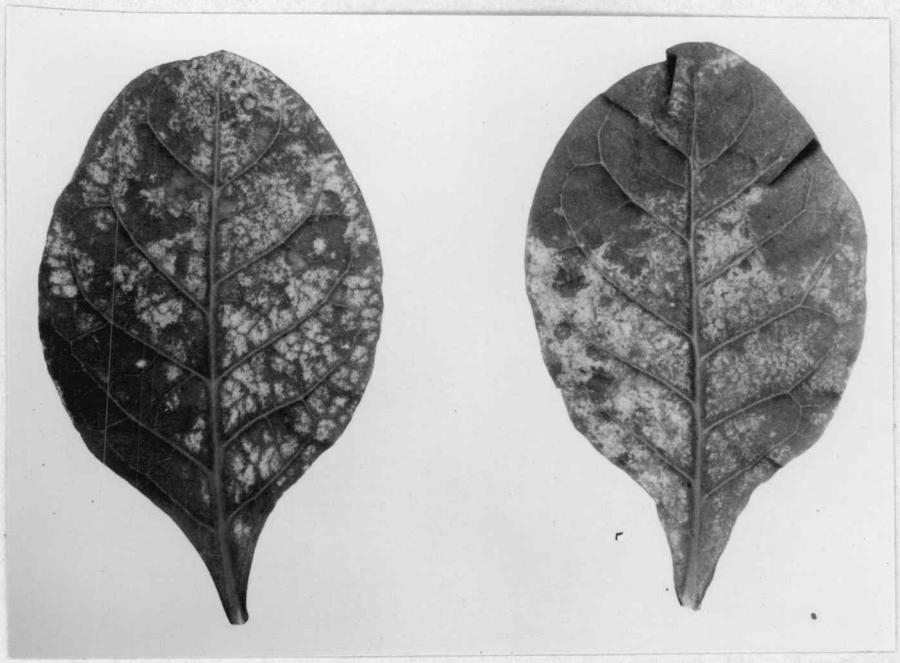


Fig. 1

Plate 32

Plate 33

Fig. 1. A leaf from *Nicotiana sylvestris* showing symptoms due to infection of Canada-streak virus, free from X. Notice that practically only yellow blotches are evident.

Fig. 2. A leaf from *N. sylvestris*, showing symptoms due to infection of Canada-streak virus, free from X. Inoculations from plants manifesting symptoms as shown in fig. 1, produced similar symptoms in potato as when inoculations were made from plants showing considerable necrosis.

Fig. 1

Fig. 2

Plate 33

Plate 34

Fig. 1. Leaflet from Bliss Triumph infected with Canada streak, as a result of juice inoculations from an infected Jimson weed plant.

Fig. 2. Leaflet from an Arran Chief plant infected with Canada streak. Note the severe necrosis.

Fig. 3. Leaflet from an Arran Victory infected with Canada-streak virus showing only a pronounced variegated type of mottling; some of the leaves from the same plant showed necrosis.

Fig. 4. Leaflet from President plant showing a chlorotic blotchy type of mottling due to infection of Canada-streak virus. Some of the intermediate leaves from the same plant showed foliar necrosis.

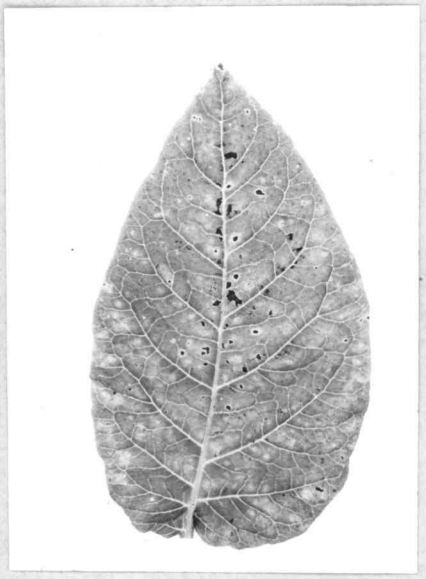


Fig. 1

Fig. 2

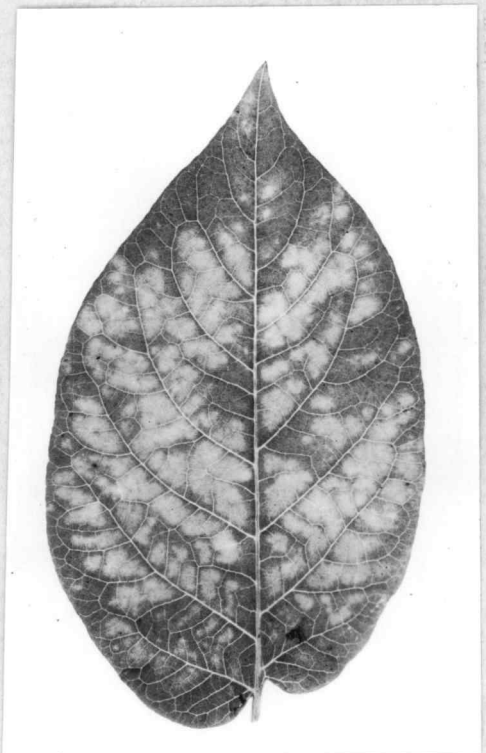


Fig. 3

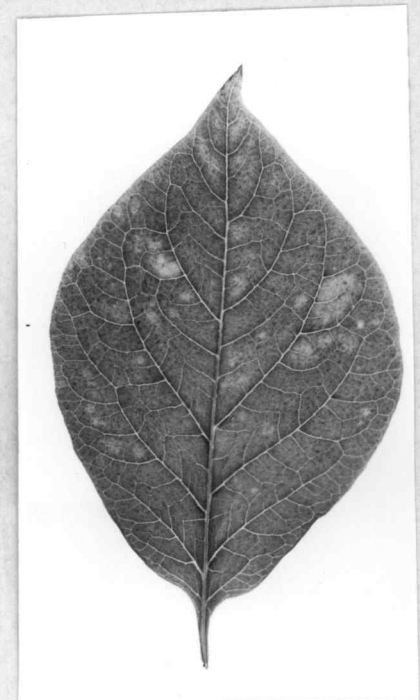


Fig. 4

Plate 34

Plate 35

Fig. 1. Majestic plant showing current season infection of Canada streak.

Fig. 2. Arran Chief plant showing severe necrosis and leafdrop due to current season infection of Canada streak.

Fig. 3. Earliest of All plant showing second-generation symptoms of Canada streak, consisting of a yellow mottling and considerable foliar necrosis.

Fig. 4. Arran Victory plant showing second-generation symptoms of Canada streak. Considerable necrosis is evident especially on the intermediate leaves.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Plate 35

Plate 36

Fig. 1. Bliss Triumph plant showing current-season-infection symptoms of Canada streak. Note the necrosis and leafdrop.

Fig. 2. Early Rose plant showing necrosis and leaf-drop due to current season infection of the Canada-streak virus.

Fig. 1

Fig. 2

Plate 36

Plate 37

Fig. 1. Internal symptoms of tubers of different varieties infected with Canada-streak virus. Note that the parenchyma tissue rather than the vascular region is affected. The seed-pieces are derived from infected tubers of the following varieties: 1, Seedling 41956; 2, Sebago; 3, Irish Cobbler; 4, President; 5, Arran Victory; 6, Chippewa; 7, Green Mountain; 8, Bliss Triumph.

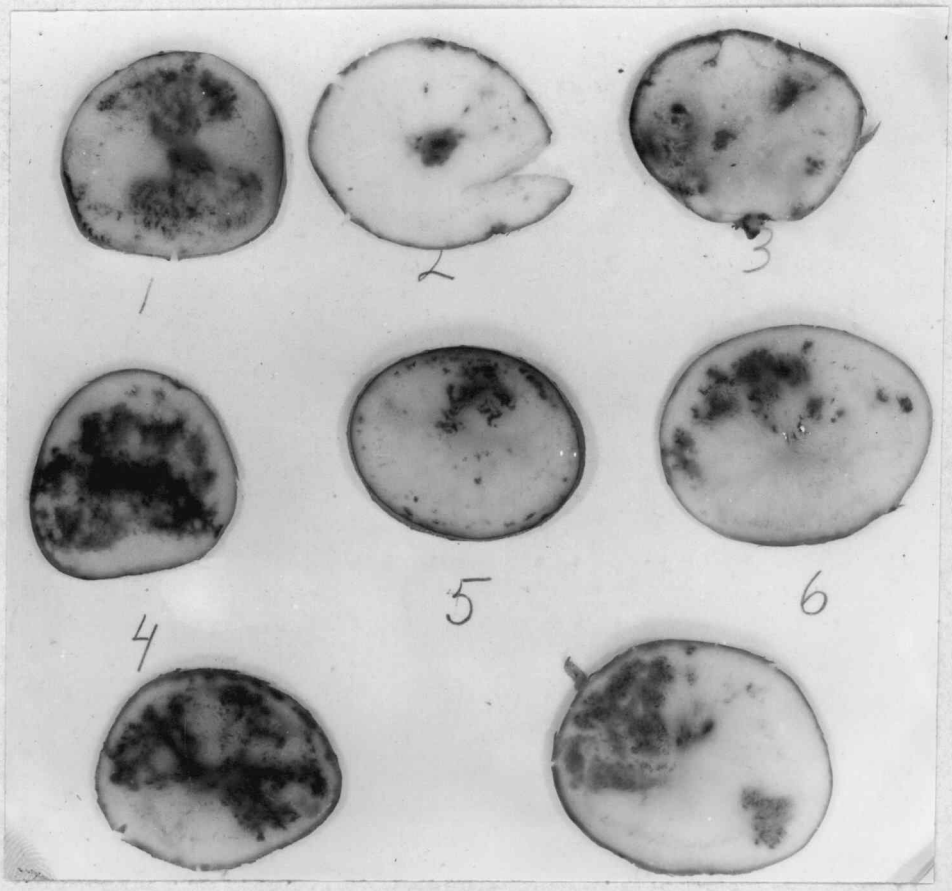


Fig. 1

Plate 37

Plate 38

Fig. 1. Leaf from pepper plant infected with Calico.

Fig. 2. Leaf from N. sylvestris infected with Calico.

Fig. 1

Fig. 2

Plate 38

Plate 39

Fig. 1. Pepper plants infected with Calico were inoculated with viruses belonging to the Aucuba-mosaic group, to determine whether the presence of the Calico virus in the pepper affords protection against infection. The following plants are representative samples taken from the different series which were inoculated: A, tuber blotch; B, pseudo-net necrosis; C, Aucuba mosaic; D, Canada streak; E, Calico-infected pepper plant not inoculated. The fact that all inoculated plants became infected with the respective viruses, shows that Calico is not closely enough related to these viruses to provide protection.

Fig. 1

Plate 39