A Study of Certain Viruses Pathogenic to the Tomato[1]

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Fig. 1

Fig. 2

Fig. 1. Streak of tomato following artificial inoculation in greenhouse. Photographed March 2, 1916, at Lafayette, Indiana, by George Osner.

Fig. 2. Distortion and malformation of young leaves of tomato plant infected with virus A.

Introduction

Winterblight or streak has been recognized as a transmissible virus disease of tomato in Indiana since 1916, (Fig. 1). It occurs mostly on greenhouse tomatoes, appearing in the initial stages as a necrotic spotting of the leaves and necrotic streaking of young stems and petioles. The tips of shoots are frequently killed. Subsequent symptoms are conspicuous mottling, distortion and malformation of leaves that develop subsequent to the necrotic phase, and stunting of the plants. Once the disease starts in a greenhouse planting, it usually spreads rapidly. Crop loss is complete if the disease develops before the tomato plants have attained any size or set much fruit.

As has been repeatedly demonstrated, this disease may be produced by a combination of the virus of tobacco mosaic (Johnson's tobacco virus 1 (23)) and a virus present in all tubers of many American varieties of potatoes (Johnson's tobacco virus 5 (23)). As considered here, it is essentially a double-virus disease in which the two viruses act in com-

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plementary fashion to cause a more destructive disease than either virus alone will produce. This property of complementary action has been used by the writer to separate a number of viruses into two opposing groups. Each member of one group is complementary to the potato virus so far as its streak-producing property is concerned. The tobacco mosaic virus is a typical example of this group. Each virus of the second group is complementary to the tobacco mosaic virus. The virus from apparently healthy plants of many old American potato varieties is a typical example. For convenience, the first group is referred to as the virus A group, and the second as the virus B group.

The purpose of this paper is to present references to the pertinent literature and a brief account of some studies by the writer on the symptoms, host range, and properties of two viruses of the B group involved in the tomato streak complex.

Literature on the Double-Virus or Streak Disease of Tomato

The earliest reference that the writer has found to tomato streak is apparently in Plowright's writings of 1887 (28). The following workers, listed in chronological order from 1888 to 1931, also report work on the streak or winter-blight disease: Galloway (11), Lodeman and Bailey (3), Selby (37), Clinton (7), Orton and McKinney (27), Howitt and Stone (18), Gardner and Kendrick (13), Gardner (12), Dickson (8), Johnson (21, 22), Vanterpool (43), Gardner and Kendrick (14), Blood

Fig. 3

Fig. 4

Fig. 3. Jimson weed plant 23 days after inoculation with virus B, showing sequence of vein-clearing on older leaves, transverse bands of mild chlorosis and vein-banding on next younger and still younger leaf tissues, respectively, and irregular mottling barely visible on the younger leaves.

Fig. 4. Jimson weed plant 17 days after inoculation with the Jimson weed strain of virus B, showing the more severe disease produced by this virus.

(5), Berkeley (4), Stover (39), J. Henderson Smith (17), Jarrett (19), Doolittle and Blood (9), Valleau and Johnson (40, 42.)

Clinton (7) probably was first to report artificial transmission of the disease. Vanterpool (Dickson, 8) and Johnson (21, 22) demonstrated its duplex nature. Gardner and Kendrick (14) showed by inoculation tests that it is produced by a combination of the tobacco mosaic virus and the virus present in apparently healthy potato plants, namely the virus of Fernow's mosaic B (10) and herein designated as virus B.

The Virus A Group

The strain of tobacco mosaic used for most of these studies with references made as virus A exhibited the properties of Johnson's tobacco virus 1 (23) such as resistance to drying, ageing, heat, dilution, and chemicals and produced typical tobacco mosaic symptoms on tobacco (1, 15) and tomato (13), (Fig. 2). In addition, a number of viruses were collected in tomato fields which gave strikingly different symptoms when inoculated into tomato alone but which produced typical tomato streak when combined with a B virus. That there should be a number of viruses of the A type is evident from the work of Henderson Smith (16), Jarrett (19), and Valleau and Johnson (40).

The Virus B Group

The individual viruses of the B group are characterized by their complementary action in the production of tomato streak when combined with virus A. Two in particular are of concern here. The first is evidently the one which has been referred to by other workers as the mottle or ringspot virus (22), healthy potato virus (41), mosaic B (10), and latent virus (6). The symptoms produced on tomato by the virus used in most of the writer's experiments compare best with those described by Burnett and Jones (6) as produced by their latent potato virus. On tobacco it has produced symptoms most comparable with Johnson's mottle virus. On Jimson weed (Fig. 3) it produces symptoms most like those figured by Fernow for his mosaic B.

The second virus was originally collected from a wild Jimson weed. It is more virulent than the potato virus and is best distinguished from the latter by the much more severe disease it produces on Jimson weed (Fig. 4) and *Nicandra physalodes*. When combined with virus A, it produces typical streak, thus marking it as a virus of the B group.

Literature on the virus B group.—Many workers have transmitted or attempted to transmit potato virus diseases to tomato. The following papers may be mentioned: Johnson (22, 23), Quanjer (29), Schultz and Folsom (35), Olitsky and Northrop (26), Fernow (10), Vanterpool (43), E. M. Johnson (20), Valleau and Johnson (41), Koch (25), Burnett and Jones (6). The following viruses have been described from apparently healthy potatoes: Virus of mosaic B (Fernow), spot necrosis and ringspot (Johnson), veinbanding and healthy potato (Valleau and Johnson), and latent and virulent latent (Burnett and Jones). Johnson's spot necrosis has been split into a mottle virus and an insect-transmitted virus by Koch. The veinbanding virus is probably the same as Koch's

insect-transmitted virus. Valleau and Johnson and Burnett and Jones were unable to produce streak in tomato by combining it with virus A. The ringspot virus is apparently the same as Valleau and Johnson's healthy potato virus and Burnett and Jones' virulent latent virus. All of the above viruses, except that of veinbanding, appear to have a factor in common which combines with virus A to produce streak in tomato. Fernow's description of his mosaic B and Johnson's description of his mottle virus appear to fit this common factor which is designated here as virus B.

Symptoms produced by virus B.—Goldstein (15) has described a series of leaf symptoms that appear consistently on tobacco plants inoculated with the tobacco mosaic virus. An analogous set of symptoms is produced by virus B on tomato, Jimson weed, and tobacco. They appear on Jimson weed (Fig. 3) as veinclearing on the older leaves, general chlorosis with green islands on next younger tissue, and veinbanding on still younger tissue. Each of these more or less transverse bands of symptoms grades into the other with no sharp line of demarcation. All leaves that develop subsequent to those that show the veinbanding show irregular chloritic areas between the major veins. The same sequence of symptoms develops on tomato and tobacco plants infected with virus B but is not so obvious.

Susceptibility of species and varieties of the Solanaceae to virus B.—Virus B was inoculated into the following 20 species and varieties of the Solanaceae: *Browallia elata* L.; *Capsicum frutescens* L., var. *Cayenne; Datura stramonium* L., (Jimson weed); *Lycopersicon esculentum* Mill., var. *Greater Baltimore; Lycopersicon pimpinellifolium* Mill.; *Nicandra physalodes* (L.) Pers.; *Nicotiana alata* Link and Otto, var. *longiflora; N. Sanderae* Sanders; *N. sylvestris* Spegaz, and Comes; *N. tabacum* L.; *Petunia hybrida* Vilm., vars. *Calif. Giant* and *Gen. Dodds; Physalis Alkekengi* L.; *P. pubescens* L.; *P. subglabrata* Mackenzie and Bush.; *Solanum carolinense* L.; *S. Melongena* L., vars. *Black Beauty* and *Neapolitan; S. nigrum* L.; *P. pseudocapsicum* L.; *S. tuberosum* L. (seedlings). It was recovered in apparently unaltered form from nineteen of the twenty. *S. pseudocapsicum* was not infected.

Mottling was produced on all plants from which the virus was recovered except for certain potato seedlings which showed no symptoms. Necrosis was produced on *N. physalodes*, pepper, and certain potato seedlings. The virus was recoverable only from the necrotic lesions of potato seedlings showing no other symptoms. It was recovered readily from the necrotic lesions on cayenne pepper but only occasionally from other parts of such infected plants.

Properties of virus B.—Virus B remained infectious after storage for 87 days in Jimson weed juice in the refrigerator and for 47 days at room temperature. In one test, virus B in tomato juice was still infectious after dilution to 1:10,000 but not 1:100,000. The inoculum was applied to the test plants with the broken point of a small glass pipette. The virus withstood drying for 16 days in Jimson weed leaves but not for 18 months. It survived heating at 61°C. for ten minutes but not 70°C.

Symptoms produced by the Jimson weed strain of virus B.—The striking symptoms produced by the virus from Jimson weed on tomato, Jimson weed (Fig. 4), certain species of tobacco, and *Nicandra physalodes* and the fact that it combines with virus A to produce streak have made it of special interest. The sequence of development of symptoms produced by this virus is much the same as that for virus B from potato, but the ultimate effects of the virus are much more severe. Clearing of the veins on the older leaves is quickly followed by a necrosis of the cleared veins, with necrosis extending into the interveinal areas. The general chlorosis of the next younger tissue is quickly followed by extensive necrosis of this same zone, producing a burned or scorched effect. Marked interveinal chlorosis and veinbanding develop on the next younger leaves with some necrotic spotting and rugosity. All leaves that develop later than these are coarsely mottled and more or less cupped, puckered, or savoyed.

Host range and properties of the Jimson weed strain of virus B.—The Jimson weed virus was used for inoculation and recovered unchanged from the same series of solanaceous hosts as virus B. The severity of the disease produced on Jimson weed, *Nicandra physalodes* and *Nicotiana alata*, in particular, served to differentiate it from virus B. The virus was infectious after 87 days storage in Jimson weed juice in the refrigerator and after 16 days drying in Jimson weed and tomato leaves. It withstood heating at 75°C. for ten minutes, being more resistant to heat than virus B, and was infectious at a dilution of 1:10,000 but not 1:100,000.

Separation of the Component Viruses of Tomato Streak

In the course of the limited host range studies with the three viruses of concern in this paper, it was found that certain hosts could be used to separate out the viruses present in the streak complex. Virus A could be recovered only from the necrotic lesions on Jimson weed and certain potato seedlings inoculated with this virus. It was recovered from necrotic lesions on inoculated Black Beauty eggplant *(Solanum melongena)* and only occasionally from non-necrotic parts. It could be recovered from most portions of infected pepper plants. The B virus, on the other hand, could be recovered from all parts of Jimson weed plants inoculated with these viruses and from symptomless or mottled parts of the potato seedlings used in the studies. It was found possible to recover either B virus from Jimson weed or potato seedlings inoculated with streak. Virus A could be recovered from pepper inoculated with streak. The entire streak complex was sometimes recovered from non-necrotic parts of both Black Beauty eggplant and pepper. It appears that virus A invades this eggplant less extensively than the B viruses and that the latter do not become systemic in pepper to the same extent as virus A.

Summary

A number of viruses or strains of viruses of the tobacco mosaic group occur on canning tomatoes in Indiana. This conclusion is based on symptoms produced by various collections of these viruses and by their

complementary action with the so-called healthy potato virus or virus B in the production of tomato streak. Likewise, it appears that there are a number of viruses and strains of the virus B group, two of which are described in some detail. The differences in the extent to which the viruses of these two groups invade Jimson weed, Black Beauty eggplant, certain potato seedlings or clones, and pepper provide a means of their separation from a streak complex. The variety of forms and relative abundance of these viruses as they occur in Indiana justify additional investigations now under way.

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