THE IDENTITY AND HOST RELATIONS OF THE LATE-BREAKING VIRUS

by

WILLIAM BRUCE RAYMER

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APPROVED:

Redacted for Privacy

Professor of Plant Pathology

In Charge of Major

Redacted for Privacy

Chairman of Department of Botany and Plant Pathology

Redacted for Privacy

Chairman of School Graduate Committee

Redacted for Privacy

Dean of Graduate School

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Typed by Calista Crimins

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INTRODUCTION

In 1946 a disease of potatoes new to Oregon appeared in most fields of Netted Gems, Burbanks, and White Rose. A study of the disease by Milbrath and English (59) resulted in its characterization and application of the name "late-breaking virus disease" of potatoes. The name derives from the fact that symptom expression in infected plants usually occurs late in the season. Certain characteristics of the disease distinguished it from previously described diseases but related it to the following group of potato virus diseases: purple-top wilt, yellowtop, witches' broom, apical leafroll, haywire, and bunch-top.

In 1952 this disease became epiphytotic in central Oregon where 40-50 per cent of the plants in some fields were infected as compared with the high of 3 per cent noted in 1946. Further study of the disease was necessary to determine the reason for this severe outbreak and to obtain additional basic information on the virus responsible. Preliminary field observations by Dr. J. A. Milbrath and Mr. Clark Amen, plant pathologist and entomologist respectively, suggested that the virus was being carried into the potato fields from outside sources, in contrast to most potato viruses which are brought

into the field in the tubers. There was no correlation between the field incidence of the disease and the seed lots involved. Dr. Milbrath noted virus-like disorders suggestive of aster yellows in Ladino clover (Trifolium repens L.) and certain weeds adjacent to potato fields which showed high incidence of the late-breaking disease and suggested that Mr. Amen survey the fields for vectors of the aster yellows virus. Mr. Amen found fairly large numbers of the aster leafhopper (Macrosteles fascrifrons Stal.), a known vector of the aster yellows virus (34), on the Ladino clover.

From preliminary tests with leafhoppers collected in these fields Raymer and Amen (66) reported that late-breaking symptoms were produced in White Rose potato plants and aster yellows symptoms were produced in aster plants on which the leafhoppers were allowed to feed. A further investigation of the late-breaking disease was now possible in which graft transmission of the causal virus could be supplemented by insect transmission studies. Graft transmission of viruses is a non-selective method and will permit all viruses present in a scion to be transmitted to the stock. The common viruses present in potatoes and other potential hosts of the late-breaking virus could now be eliminated from the virus cultures by using the aster leafhopper as a means of transmission since

this insect is only known to transmit the aster yellows virus. As a further advantage, insect transmission is not limited to those plants in which satisfactory graft unions take place.

The ultimate objective of most disease studies is to determine a means of control. To attain this objective, certain basic information was necessary on the relationship of the late-breaking virus to potato, other hosts, the vector, and similar viruses. The purpose of this study was to obtain such information on the following points:

(1) the relation of the late-breaking virus to similar diseases on the basis of their causal viruses;

(2) the vector relationship of the aster leafhopper;

(3) the relation of phyllody in Ladino clover to late-breaking in potatoes;

(4) the host range of the late-breaking virus, particularly those legumes or weeds which could maintain the virus over-winter and thus act as reservoirs of the disease;

(5) the tuber perpetuation of the virus as a factor in identification and incidence of the disease;

(6) the determination of time of infection in potato fields;

(7) the effect of environmental conditions on symptom expression of the disease in potato.

LITERATURE REVIEW

Literature concerning those viruses which most closely resemble the late-breaking virus is reviewed. Symptoms, host range, and mode of transmission are stressed since these points are the basis for differentiation of the viruses and diseases considered.

Aster Yellows Virus

Smith (82, p.20) first described aster yellows in 1902 but did not demonstrate its virus nature.

In 1924 Kunkel (34) showed that aster yellows was a virus disease and reported transmission of the causal agent with the aster leafhopper, Macrosteles fascifrons Stal. (Cicadula sexnotata Fall., C. divisia Uhl.).

In his classical study of the aster yellows virus, published in 1926, Kunkel (35) established a host range of 64 species of plants in 21 different families. Most of these species were composites and only two were solonaceous.

Kunkel (36) also distinguished between aster yellows and the potato witches' broom virus on the basis that the latter was not transmitted by the aster leafhopper.

Severin (72, pp.550-570), working in California, reported a yellows disease of celery (Apium graveolens L.

var. dulce Pers.), lettuce (Lactuca sativa L. var. capitata L.), and other plants. He was able to transmit the causal virus by means of the aster leafhopper to aster (Calistephus chinensis Nees), in which it produced symptoms typical of aster yellows (34). The same virus was transmitted to aster and celery from zinnia (Zinnia elegans Jacq.). Sugar beet (Beta vulgaris L.) was not susceptible to California aster yellows and aster was not susceptible to the sugar beet curly top virus.

A celery yellows from Maine similar to the one in California was reported by Folsom in 1929 (15, pp.25-29). No transmission trials were made.

Kunkel (37) found a disease resembling aster yellows in tomato (Lycopersicon esculentum Mill.), which was prevalent in Maryland during 1930. His attempts to transmit the New York aster yellows to tomato by means of the aster leafhopper failed, but graft inoculations from diseased Nicotiana rustica L. were successful.

In further experiments, Kunkel (38, pp.90-120) was unable to transmit eastern (New York) aster yellows to Jimson weed (Datura strammonium L.), tobacco (N. tabacum L.), or peach (Prunus persica (L.) Batsch), either by grafting or insect inoculation. Of the 170 species in 38 families to which the known host range had been

expanded by Kunkel, none were legumes. Among those species apparently immune from the New York aster yellows when inoculated by means of the insect were celery, zinnia, and potato.

Kunkel (39) made a comparison of California aster yellows and New York aster yellows and concluded that they were not identical. Although no difference in the symptoms of the two viruses on aster could be detected, the New York virus could not be transmitted to either celery or zinnia while the California strain was readily transmitted to these hosts.

The host range of the western (California) aster yellows virus was extended to several ornamental species in 1934, which demonstrated the same wide host range potential that had been found for the eastern strain (79).

Severin (74, pp.320-325) made a comparative study of aster yellows from several states, including the New York aster yellows from Kunkel in 1934. Although he was able to infect 6/122 celery plants with the New York aster yellows, Severin concluded that celery was highly resistant to all the viruses tested with the exception of the California strain. The leafhopper, Colladonus montanus Van Duzee, (Thamnotettix montanus Van Duzee) was unable to transmit the New York strain

of aster yellows to either aster or celery although this insect had been shown to be a vector of California aster yellows.

The first report of transmission of aster yellows to potato was by Severin and Haasis (78, pp.330-335) who infected Bliss Triumph and White Rose potatoes with the California strain by means of the aster leafhopper. The symptoms closely resembled those later described for purple-top wilt. All attempts to recover the virus from potato plants with the aster leafhopper failed, nor was the virus recovered from tubers of the plants infected. No natural field infection of potatoes in California had been noted at this time.

Purple-top wilt or similar diseases of the potato became prominent in many potato-producing areas about 1935 (48), but no connection with the aster yellows virus was made with the exception of the work of Severin and Haasis. Purple-top wilt was characterized in the following manner: First symptoms of the disease appeared only after the plant was well developed and consisted of an upward rolling of the terminal leaflets, especially near the base. Terminal growth ceased and the rolled leaflets of pigmented varieties assumed a purplish color. Abnormal development of shoots from axillary buds occurred shortly after the above symptoms appeared. Axillary tubers were

produced by enlargement of the base of such abnormal shoots. Within two weeks after symptoms first appeared, the infected shoots wilted and died. A pronounced necrosis of the vascular bundles at the base of the stem was always present.

Long (49) indicated that purple-top wilt had been known in North Dakota since 1928. His observations over a number of years showed that hair-sprout tubers were closely associated with the purple-top disease. He also determined that the number of infected plants increased markedly in the later portion of the growing season.

Orton and Hill (64) reported a disease resembling purple-top wilt in West Virginia which they described as "blue-stem" due to the pigmentation of infected plants of the Rural variety. An intense brown discoloration of the tuber at the point of stolon attachment was associated with the blue-stem disease as well as a less intense net-necrosis of the storage parenchyma. This same severe necrosis was noted in the stems and roots as well as the tubers. Blue-stem (purple-top wilt) was not perpetuated in the tubers from infected plants. The disease was first noted near the borders of the fields and was very rare when muslin cages were placed over the plants, which indicated that the virus was transmitted by insects. A detailed histological study of the disease in potatoes was made.

Brentzel's (6) detailed observations of purple-top wilt in North Dakota indicated that early planted potatoes of the Triumph variety suffered no apparent loss in yield although 20 per cent of the field developed the late wilt symptoms. In late planted fields, the infected plants had tubers noticeably smaller than normal.

The same disease was reported from New York in 1939 by Decker (12) who emphasized the difference in symptoms on different varieties due to the presence or absence of the pigmentation factor.

Leach (47) was able to produce purple-top wilt of potatoes in plants caged with aster leafhoppers collected from many sources. Unfortunately, some of the caged check plants which were not exposed to insects also developed the disease. Leach found that the disease was not transmitted through the tubers nor were tubers from infected plants more subject to spindling-sprout than the progeny of healthy plants.

Muncie (61) noted that purple-top wilt was generally distributed throughout the state of Michigan and that the disease appeared to be identical with the one known as "moron" since 1915.

The only recovery of the aster yellows virus from infected potatoes with insects was made by Severin (75)

with a long winged strain of the aster leafhopper found in certain areas of California.

Burke (7) in reporting incidence of purple-top wilt in different potato varieties, considered the characteristic stem-end necrosis of the tubers to be a valuable diagnostic character. Varieties were classed as very susceptible, medium in susceptibility, and least susceptible. Green Mountain and Russet Rural were placed in the first category, Chippewa and Katahdin in the second, and Cobbler, Mesaba, Sebago, and Pontiac in the third. Sebago showed fewer tuber symptoms than any of the other varieties.

Conclusive evidence that purple-top wilt of potato could be caused by the New York aster yellows virus was presented by Epps (14) in 1942. This virus was obtained by grafting potato to Niotiana rustica, feeding the aster leafhopper on infected N. rustica, and then transmitting the virus to aster and potato by means of the insect. Symptoms of aster yellows were produced in N. rustica and aster, and purple-top wilt symptoms in the potatoes. Epps found that the New York aster yellows virus overwintered in the ox-eye daisy, (Chrysanthemum leucanthemum L.) and broad leaved plantain (Plantago major L.).

This work was confirmed by Younkin (92, pp.179-183) who used a strain of aster yellows from ragweed (Ambrosia

artemisifolia L.). He found that transmission of the virus from potato to N. rustica was most frequently accomplished by inarch grafting. Transmission of aster yellows to the potato by means of the aster leafhopper was most readily accomplished by using 10 insects per plant with a test feeding period of seven days. Tuber perpetuation was rare. Symptoms resembling aster yellows were obtained in four of 198 N. rustica plants cleft-grafted with scions from diseased potato plants. Colonies of virus-free aster leafhoppers transferred the virus from these infected plants to aster, N. rustica, and potato, in which plants symptoms of aster yellows were produced. However, the N. rustica plants inoculated directly from potato by grafting began to wilt 10 days after symptoms appeared and soon died, which was not typical of aster yellows. Phloem tissues of all plants inoculated with the strains from potato were necrotic, but this necrosis was not noticeable in plants inoculated with the ragweed strain. In these experiments, almost half of 475 potato plants were infected with the aster yellows virus. Younkin rated the susceptibility of 11 varieties similar to Burke but based his diagnosis on aerial symptoms rather than tuber symptoms.

In North and South Dakota, areas exist where aster yellows may be very prevalent on carrots but purple-top

wilt of potatoes is rare. For this reason Tervet (83) believes that purple-top in these areas is probably not due to the aster yellows virus.

Kunkel (43) received two samples of carrots with almost identical yellows symptoms from Texas. The virus present in one sample was transmitted to carrot and aster, but not to celery or zinnia by means of the aster leafhopper, and was therefore considered to be typical aster yellows. The virus present in the other sample of carrots could not be transmitted by the aster leafhopper but was transmitted to potato, tomato, carrot, red clover (Trifolium pratense L.), and other plants by means of dodder (Cuscuta campestris Yunk.). The virus could not be distinguished from aster yellows on carrot or periwinkle (Vinca rosea L.).

Leach and Bishop (48) made a complete study of the purple-top disease in West Virginia and confirmed the results of other workers. The aster yellows virus could not be recovered from infected potato plants, nor transmitted from potato to potato by means of the aster leafhopper. There was always necrosis of the vascular elements at the base of the stem which often spread to the stem end of the tuber associated with purple-top wilt. The incubation period of the disease in potatoes was from 34-68 days.

Dana (11) reported transmission of the phyllody condition in common bean by means of cleft grafting in 1947. The disease was found in Eastern Oregon on varieties of bean resistant to the curly top virus as well as on susceptible varieties. He indicated that the disease was apparently induced by the aster yellows virus which was found in the area on many ornamental plants.

Jensen and Tate (32) in Nebraska were unable to produce current season symptoms of purple-top wilt in potatoes inoculated by means of the aster leafhopper. When tubers from inoculated potatoes were grown, 2/56 produced plants with symptoms of purple-top wilt. Field experiments indicated that the time of infection in nature was too late for development of symptoms before the potatoes matured.

Onion (Allium cepa L.), shallot (Allium ascalonicum L.), and gladiolus (Gladiolus gandavensis Van Houtte) were shown to be susceptible to the western aster yellows virus by Smith and Brierley (80) in 1948. Another monocotyledonous plant, canna (Canna generalis Bailey), was shown to be susceptible to the aster yellows virus by these same workers in 1951 (81).

In 1949 Milbrath and English (60, pp.465-469) described a disease of potatoes for which they proposed the

name "late-breaking virus disease." This disorder resembled purple-top wilt and similar diseases but was considered distinct on the following basis:

(1) evidence of tuber perpetuation for two or more generations;

(2) no internal necrosis of stems or tubers;

(3) tubers borne on short stolons but not in chains;

(4) profuse production of aerial tubers;

(5) uneven distribution of the virus in the tubers;

(6) hair sprouts from infected tubers;

(7) production of dwarf plants at an early date, or production of plants which develop symptoms late in the season, often from the same tuber.

Transmission of the virus by grafting from potato to potato was demonstrated.

McWhorter (54) in 1950 reported an aster yellows-like disease of alsike clover (Trifolium hybridum L.) from Oregon. The diseased plants were abnormally erect and had variously modified inflorescences. No transmission of the disease was made.

Bonde and Schultz (4 and 5) were unable to produce current season symptoms of purple-top wilt in potato with aster yellows from annual sow thistle (Sonchus asper Hoffm.). Some inoculations yielded plants with apical leafroll, a

virus shown by these workers to be distinct from purple-top wilt. Other plants in the same series produced tubers with poor germination or which gave rise to weak plants typical of purple-top wilt. No current season symptoms were produced on healthy potatoes by inarch grafting from purple-top infected plants, though the tubers from inoculated plants had weak sprouts. When scions from potatoes infected with purple-top wilt were grafted to tomato, symptoms typical of the disease in potato were produced in contrast to the downward bending and upward rolling of leaves on plants to which apical leafroll was transmitted. No perpetuation of purple-top in the tuber beyond the second generation was noted in a series of experiments over several years. The stem end discoloration of tubers from purple-top infected plants noted in other areas was not present in Maine.

Western aster yellows was demonstrated to be the causal virus of purple-top wilt in Wisconsin (71, pp.10-23). Extensive graft transmission trials from field infected potatoes to healthy potatoes and to N. rustica confirmed the results of earlier workers. Transmission of the virus with the aster leafhopper to potato was erratic.

The Lassen variety of strawberry (Fragaria chiloensis Duch.) was shown to be susceptible to the western aster

yellows virus by Frazier and Thomas (18). This is one of the few rosaceous plants known to be a host of this virus.

Raymer and Amen (67) made a preliminary report of association of the late-breaking virus disease of potatoes with a phyllody condition in Ladino clover (Trifolium repens L.) in 1954. This virus produced aster yellows in aster, celery, and other plants which indicated a relationship to the aster yellows group of diseases.

In 1955 Kunkel (45, pp.260-273) demonstrated cross protection between the eastern and western strains of the aster yellows virus. Gladiolus carrying California aster yellows was found growing in the East by Dr. Floyd Smith of Beltsville, Maryland. He sent the virus to Kunkel in aster and celery to be compared with the eastern strain. By using large numbers of leafhoppers, Kunkel was now able to transmit the eastern strain to both celery and zinnia, and thus eliminated the difference in host range of these viruses. However, he was able to distinguish between these strains on the basis of the symptoms in aster, periwinkle, and N. rustica, although in a similar previous study no such symptom differences could be detected. He stated that in aster, the western strain was more severe, produced more stunting of growth and tended to produce short fleshy side shoots in contrast to the spindly side

shoots produced by the eastern strain. In N. rustica the western strain produced a severe cabbage-head type of malformation while the eastern strain caused an elongated, upright growth habit. Short swollen side shoots were also characteristic of the western strain in periwinkle and zinnia as contrasted with the thin elongated side shoots of the eastern strain in these hosts. On tomato the symptoms were similar but the western virus caused more severe stunting and earlier death than the eastern. In transmission experiments Kunkel found that symptoms of the first virus only were evident in the plant when cross inoculations were made with the aster leafhopper. Likewise the insects transmitted only the first virus they were allowed to acquire in experiments where they fed on sources of both strains. A further point of distinction between the two strains was the fact that celery and zinnia were most readily infected with the western strain.

Phyllody of Ladino clover was reported from Maine (84) in 1955 and it was suggested that the clover in that area might act as a reservoir for the aster yellows virus as had been reported from Oregon.

A summary of the very extensive work on the insect relations of the aster yellows virus is necessary to an

understanding of the problems of identity, host range, and control of the virus in the field.

Only the aster leafhopper is known to transmit the eastern aster yellows virus while a total of 22 vector species have been reported for the western strain by Severin (76 and 77). He considered this to be evidence for the non-specific transmission of this virus. The aster leafhopper is not known to transmit any virus other than aster yellows but some of the vectors of the western strain also transmit some stone fruit viruses (31).

Multiplication of eastern aster yellows in the aster leafhopper has been demonstrated conclusively by Maramorosch (52). A latent period for the virus in the leafhopper of from nine days to several weeks depending on the temperature has also been demonstrated (38). High temperatures have been shown to inactivate the virus in both leafhoppers and plants and to cause the production of mild strains of the virus in the insects (40, 41 and 42).

Aster yellows virus may be transmitted under specific conditions, from leafhopper to leafhopper by hypodermic inoculation with a suspension of crushed leafhopper bodies, but no such transmission to plants has been made (3). From a study of the physical properties of such suspensions of crushed viruliferous insects, Black (2)

concluded that virus activity was associated with a relatively unstable particle of large size as compared with plant viruses previously studied.

Control of aster yellows in many crops, including potatoes, has been demonstrated in many instances (25, 35 and 65). Control with insecticides such as DDT has been most successful for those crops in which the vector breeds. The potato is a poor host for the aster leafhopper (75).

Apical Leafroll Virus

In 1929 Schultz and Bonde (70) described a new potato disease to which they applied the name "Apical Leafroll." The apical leaves of infected plants manifested a rolling similar to primary leafroll. Succeeding generations from infected tubers continued to display symptoms mainly confined to the upper leaves, which distinguished the disease from primary leafroll. As compared with potato witches' broom, apical leafroll plants were taller, more vigorous and had fewer shoots. Tubers on apical leafroll plants were frequently clustered close to the stem on short stolons in the manner of witches' broom but though reduced in size were normal in shape and number. Apical leafroll was readily transmitted to healthy potatoes by means of tuber grafts. Symptoms of the disease characterisically appeared late in the

growing season even when infected tubers were involved, a further point of differentiation from leafroll.

In 1947 Bonde and Schultz (4) reported transmission of a disease similar to apical leafroll by the aster leafhopper. Symptoms were somewhat similar to purple-top wilt but differed in the following characteristics:

(1) Plants did not wilt and die prematurely.

(2) There was no pronounced necrosis of vascular bundles at the ground line.

(3) None of the tubers became flabby or developed vascular discoloration.

(4) Tubers germinated normally and the disease was perpetuated through the tubers with no diminuition of symptoms.

Bonde and Schultz (5, pp.15-30) in 1953 differentiated purple-top wilt from apical leafroll in the following manner:

(1) Tubers from apical leafroll plants were somewhat smaller than normal but remained firm and germinated normally in the spring to produce plants which at first appeared more erect and darker green than normal. Tubers from purple-top plants became soft and spongy and either failed to germinate or produced weak sprouts. If the sprouts persisted the plants were weak-appearing at first but later showed complete recovery. Secondary tubers were

often formed on mother seed pieces of purple-top tubers with no other sprouts being formed. The necrosis of the stem-end associated with purple-top in some areas is not found in Maine.

(2) Apical leafroll was perpetuated from year to year in the tubers with only slight reduction in severity of symptoms. Purple-top, on the other hand, appeared to be self-eliminating since the tubers either did not germinate or if plants were formed they showed complete recovery by the end of the season.

(3) Apical leafroll was transmitted from potato to potato by means of the aster leafhopper. Attempts to transmit witches' broom and purple-top wilt from potatoes by means of this vector failed. A source of aster yellows from oxeye daisy (Chrysanthemum leucanthemum L.) produced an apical leafroll-like disease in potatoes and aster yellows symptoms in aster but was not transmitted to celery. Apical leafroll from potato did not produce aster yellows in 46 asters tested although symptoms of apical leafroll were produced in potatoes inoculated from this source. One of the 46 asters inoculated with apical leafroll by means of the aster leafhopper became chlorotic. Field collected leafhoppers which had been allowed to feed on a source of aster yellows transmitted witches' broom to one out of five potatoes inoculated.

Bunch-Top Virus

In 1954 MacLeod (51) reviewed the literature on aster yellows (Purple-top) of potatoes and included the bunch-top disease found in New Brunswick. In his study of the bunch-top disease which closely resembles purple-top wilt, MacLeod was unable to transmit the virus by means of the aster leafhopper. However, he was able to transmit the virus by grafting to potato, Jimson weed, tomato, N. glutinosa L., N. rustica L., and Samsun tobacco, as well as to several other solanaceous species. Bunch-top virus was also transmitted to the above mentioned susceptible hosts by means of dodder, (Cuscuta gronovii Wild.). Capsicum annuum L., Solanum dulcamara L., and Solanum nigrum L. var. nudiflorum were not infected in these tests. A virus from field grown plants of Asclepias syriaca L., Erigeron canadensis L., Jimson weed, Physalis floridana L., Petunia Hybrida Vilm., eggplant (Solanum melongena L.), tomato, and Red clover produced symptoms of the bunch-top disease when transmitted to tomato and potato by means of dodder.

The bunch-top virus was not perpetuated in the tubers beyond the second generation of plants. Infected tubers often did not germinate, or germinated as late as 12 to 30 months after harvest. Some tubers from infected plants did not carry the virus while others were infected in

portions only. A "hair sprout" condition was associated with some tubers. Weak, spindling plants would develop from some infected tubers while relatively vigorous plants with symptoms resembling the "haywire" described by Goss (24, pp.7-14) would develop from others. When scions from these "haywire" plants were placed on tomato and potato, typical bunch-top symptoms developed. In combination with the leafroll virus a very severe bunch-top condition was obtained and the tubers displayed a severe net-necrosis not noted when the bunch-top virus was present alone.

When certain varieties of tomato were infected with the bunch-top virus by stem grafting from potato, symptoms resembling the tomato big bud disease were sometimes produced. These symptoms included enlargement of the terminal shoots and a tufted appearance in mature and pruned plants which resulted from proliferation of lateral shoots.

Aster yellows found in aster, carrot, and buckwheat was not transmitted to tomato or potato with the aster leafhopper in vector trials associated with this work.

MacLeod concluded from his experiments with the bunch-top virus that it was somewhat related to the aster yellows virus but considered it an aberrant strain or a different virus based on the following characteristics:

(1) the apparent inability of the aster leafhopper to act as a vector for this virus;

(2) transmission of the virus to Jimson weed, N. glutinosa L., and tobacco, which have been considered immune to the aster yellows virus by Kunkel (38, pp.90-120);

(3) a third point not emphasized by MacLeod was the fact that no legume was known to be a host for the aster yellows virus.

Haywire Virus

In 1936 Goss (24, pp.7-14) described a disease of potatoes in Nebraska known as "haywire." The sprouts from infected tubers would emerge late or not at all. Plants produced from these tubers were dwarfed and grew as a rosette. Leaflets on these plants were stiff and erect, rolled and often purplish or yellowish at the tips and margins. Aerial tubers often developed at the nodes. Tubers were few in number and set close to the stem. In some cases the underground stem was rotted and showed a grown flecking in the pith, predominantly at the nodes. The disease was transmitted to healthy potato plants by inarch grafting.

MacLeod (50) demonstrated in 1949 that a haywire effect was sometimes associated with the bunch-top virus.

Wright (87 and 88) noted nine units of potatoes with haywire-like symptoms in the Cariboo region of British Columbia. Two of these nine units were propagated in the greenhouse but no symptoms of the disease resulted except a slight stunting of the plants. No symptoms were obtained on Cyphomandra or tomato when grafted with scions from these plants.

From comparative experiments with apical leafroll, purple-top wilt, and haywire diseases, Bonde and Schultz (5, p.29) concluded that haywire was due to a distinct virus. The haywire virus was transmitted by means of plug and splice grafts to healthy potatoes where it produced chlorosis and premature death. Purple-top wilt was not transmitted by this means. Apical leafroll was readily transmitted by such grafts and the inoculated plants produced typical symptoms of the disease.

Tomato Big Bud Virus

Big bud of tomato was first characterized by Samuel, Bald, and Eardley (68) from Australia. The disease was transmitted to healthy tomatoes by means of grafts which demonstrated its virus nature. Inoculations made with expressed sap were not successful.

First indication of the disease in tomatoes was an erect growth habit of the normally recurved young fruit truss. The most distinctive symptom of the disease

was enlargement of the calyx, the segments of which remained united almost to the tips, to form a bladder-like structure. Unpruned field plants eventually assumed a tufted, rosette appearance due to the excessive development of axillary shoots from normally dormant buds. Upward rolling of the yellowish leaf margins and increased anthocyanin development in the veins of the calyx and leaves were also distinctive features of the disease. Increased thickening of the stems due to proliferation of the internal phloem was an unique diagnostic character associated with the disease. Various modifications of the floral parts occur, including a phyllody condition in which the corolla was transformed to a whorl of simple, petiolate, green leaves. Fruits which were green at the time of infection became hard, woody, and failed to ripen normally.

Solanum nigrum L., associated with field plantations of tomatoes, was often found to have symptoms closely resembling those in tomato. The virus was not transmitted to Nicotiana tabacum L. or N. glutinosa L., although diseased scions placed on these plants grew for several weeks.

These authors considered that the symptoms produced by this virus were most closely paralleled by those of the cranberry false blossom virus. Aster yellows was known

to cause less severe floral changes in its host plants. Witches' broom of potatoes was known to have little adverse effect on the blooming and fruiting of tomatoes (91) and hence was considered a distinct virus.

Michailowa (58, pp.550-558) emphasized the anatomical aspects of the disease in the Crimea where it was known as "Stowboor" or "fruit woodiness." Normally spirally thickened xylem vessels are modified to pitted elements by the virus. Bindweed, (Convolvulus arvensis L.) was found to be an additional host of the tomato big bud virus in this area.

Hill (26) reported the induction of a bunchy top condition in tobacco by the tomato big bud virus, and demonstrated the susceptibility of this host previously thought to be immune.

In 1940 Dana (9 and 10) reported the occurrence of the tomato big bud virus in the Pacific Northwest on tomato. In addition, phyllody symptoms were observed on beans, alfalfa, squash and other crops in the same area, which suggested a relationship to the big bud virus. A proliferation of the phloem was noted in diseased tomatoes. The stimulation of vegetative growth by the big bud virus was contrasted to the depression of vegetative activity and tissue necrosis associated with the curly top virus. Both viruses were present in the same general area on

several of the same host plants although there were small areas where only one or the other virus was present. Anatomical modifications due to the big bud virus found in Washington and Oregon were similar to those due to the Australian big bud virus.

In 1943 Hill (27) demonstrated transmission of the tomato big bud virus in Australia by the leafhopper, Orosius argentatus Evans (Thamnotettix argenta Evans). The virus was found in 65 species of plants belonging to 24 families under field conditions and was experimentally transmitted to 23 species in 13 families. Insect transmission to the following plants was demonstrated: tobacco, tomato, eggplant, pepper, white clover, red clover, toothed bur clover (Medicago hispida Gaertn.), and beet. Natural infection of celery and Zinnia sp. was also noted. The following plants were infected by grafting only when scions from diseased solonaceous plants were used: tomato, tobacco, eggplant, Black Nightshade, and Jimson weed. In sugar beet the disease was manifested by the production of a large number of small leaves.

The chief vector of the tomato big bud virus in the Crimea was reported to be Hyalesthes obsoletus (66).

Tomato big bud virus on potato was first reported from Yugoslavia where the incidence of the disease was especially high on various crops in dry years (23).

Menzies (55) reported two types of symptoms on tomatoes grafted with scions from purple-top wilt-like plants in Washington, one resembling those of the bunch-top disease reported from New Brunswick, and the other typical tomato big bud symptoms. No symptoms were obtained on Russet Burbank potatoes grafted with these two isolates in greenhouse tests.

Kunkel (44), working with tomato big bud from California, transmitted the virus to carrots in which bolting or premature formation of flower stalks was produced. He received bolted carrots from Menzies in Washington at an earlier date which had a milder form of big bud when transmitted to tomato by dodder.

In 1951 Giddings *et al.* (22) described a tomato disease that resembled curly top. Efforts to recover the curly top virus from these plants failed but the virus involved was transmitted to healthy tomatoes and Jimson weed by grafting. The symptoms of the inoculated plants in the greenhouse were usually mild, but occasionally became very severe. No symptoms were obtained on the following plants grafted with scions from diseased tomatoes: *Nicotiana tabacum*, *N. glauca* Graham, *Lycopersicum pimpinellifolium* (Justl.) Mill., *L. peruvianum* (L.) Mill., *N. acuminata* Hook., *Datura Meteloides* DC., *Phytolacca americana* L., and *Ricinis communis* L..

Giddings suggested that the disease might be due to a strain of the aster yellows virus although the symptoms resembled curly top more than aster yellows.

Lackey (46) made a histological study of the tomato disease described above and found definite proliferation of the phloem tissues present as compared with a phloem necrosis in the case of curly top.

Norris (62) in Australia made a major study of the disease known there as purple-top wilt of the potato and in 1954 implicated the tomato big bud virus as the causal agent. The symptoms on potato followed exactly those for purple-top wilt described in the United States as due to the aster yellows virus. The tubers from infected plants usually developed hair sprouts. Perpetuation of the virus in the tubers was demonstrated. Scions from infected potatoes were grafted to Jimson weed, on which typical big bud symptoms appeared; tomatoes were grafted with scions from the Jimson weed, and finally, potatoes were grafted with scions from the tomatoes. Transmission of the virus back to the potato was very difficult and succeeded in only one out of 51 grafts. Tuber perpetuation of the virus was found to decline rapidly from generation to generation so that this virus had completely disappeared by the fourth generation. Weak spindling plants with thin,

rounded, woody stems and swollen nodes bearing small juvenile leaves were produced from infected tubers. Conroy (8, pp.8-12) later confirmed these results.

Dr. J. D. Menzies (56) at Prosser, Washington concluded that potato purple-top in Washington is the same as the late-breaking disease in Oregon and both cause big bud in tomato.

Curly Top Virus

McKay and Dykstra (53) demonstrated the relationship between sugar beet curly top virus and the western tomato blight disease in 1927 by transmitting the curly top virus to tomato with the beet leafhopper, Circulifer tenellus Baker, (Eutettix tenellus Baker). Symptoms identical to western tomato blight were obtained and the curly top virus was recovered and transmitted to sugar beet where it produced typical curly top.

In 1929 Severin (73) reported that potato, pepper, tobacco (N. tabacum L.), and N. rustica, as well as tomato were susceptible to the curly top virus under experimental conditions. Field infection of potato and pepper was also demonstrated. The beet leafhopper was used to transmit the virus from 15 of 19 potatoes tested to sugar beets. One of these potato plants was considered by J. T. Rosa to be infected with the curly dwarf virus. Symptoms of the disease experimentally induced by Severin were

described as an inward folding of the apical leaflets as well as a yellowish coloration of these leaves and a general stunting of the plant. Dwarfed shoots were produced in the axils of leaves in advanced stages of the disease. Tuber perpetuation was not determined in these studies.

Jones et al. (33) reported infection of potato seedlings grown in test plots near Pullman, Washington, with the curly top virus. The plants were dwarfed, very erect in habit, and displayed rolling, harshness, and reddening of the foliage. A heavy infestation of the beet leafhopper on the potatoes was noted but no aster leafhoppers nor psyllids could be found. The disease was produced in plants from three tubers out of a sample of 25, which indicated a low percentage of tuber perpetuation. The curly top virus was transmitted to healthy tomatoes from these diseased potatoes by grafting.

In 1946 Milbrath (59) described Green Dwarf, a virus disease of commercial potatoes which appeared in fields throughout Oregon in amounts ranging from a trace to two per cent. The tuber perpetuated symptoms in field grown plants were an extreme dwarfing, accompanied by malformation and cupping of the upper leaves. The basal leaves remained normal except for a rosette appearance due to shortened internodes. Mature plants often reached only

six inches in height and were frequently darker green in color than normal. Late emergence of the sprouts was characteristic both in the field and in the greenhouse. Under greenhouse conditions the sprout emerges to form a dark green leafy bud which does not unfold its leaves for quite a while and the tip remained a compact cluster of dwarfed and misshapen leaves. Current season infection resulted in a cessation of growth of the affected shoot, accompanied by a dwarfing, twisting and cupping of the leaves. The disease was not sap transmissable, but was transmitted to healthy potatoes by grafting. Not all tubers from an infected plant nor all eyes of a single tuber would be infected.

Giddings (19) confirmed Severin's results by inoculating young potato seedlings with curly top virus by means of the beet leafhopper (1947). However, in tests of 91 commercial plants suspected to be infected with curly top, he was unable to recover the virus.

Menzies and Giddings (57) in 1953, working with the green dwarf virus from Washington, demonstrated that it was a new strain of curly top. This virus, designated as strain 12, was transmitted from infected potatoes, and also from tomatoes graft inoculated from diseased potatoes, to sugar beets by means of the beet leafhopper. In sugar beets no symptoms of curly top were produced.

Giddings (20 and 21), using strain 12 as well as other strains of the curly top virus, showed that potato seedlings from the variety Earlaine were susceptible to the disease. Strain 12 produced symptoms in susceptible sugar beets very slowly as compared with other strains of the curly top virus, but was more virulent to potatoes than other strains. This virus was found to move rather slowly in potatoes, which may account for the low percentage of tuber perpetuation sometimes found. Curly top was found in several fields of potatoes adjacent to leafhopper breeding areas in California.

Purple Dwarf Virus

Sanford and Clay (69) described a disease of potatoes from Alberta in 1941 as "Purple Dwarf." Plants produced from infected tubers were stunted, often darker green than normal, and showed a rosette-like growth of the foliage in the upper portion of the plant. Tuberous swellings in the axils of the leaves were sometimes present. The young leaves were typically cupped and the older leaves often rolled inwards and had purplish margins. Necrosis of the pith was not characteristic of the disease, but there was a discoloration of the phloem tissue through the stems, stolons and roots. A marked browning of the exterior vascular cylinder in the lower stem, stolons, and roots was also noted. Tubers from infected plants were small

and had a severe phloem necrosis which extended the full length of the tuber. Symptoms of the disease on plants from infected tubers either were apparent at emergence or could not be detected during the remainder of the season. The virus was transmitted to potato and N. tabacum by grafting but not to tomato.

Witches' Broom Virus

In 1954 Wright (90) reviewed the literature on the potato witches' broom virus. Symptoms on potato consisted of the following: upward rolling and marginal chlorosis of leaflets, production of elongated white stolons with numerous small tubers frequently in chains, and slender cylindrical stems formed on new tubers or stolons shortly after the appearance of foliage symptoms. In advanced stages of the disease the plants were dwarfed, chlorotic, and possessed many cylindrical stems with simple leaves.

One of the thirteen sources of the witches' broom virus used in Wright's experiments produced symptoms of the tomato big bud virus on tomato. Two other distinct strains were differentiated in these studies. No vector for this virus was known but tuber perpetuation has been demonstrated. There was some evidence to indicate that the vector was not an insect normally present in potato fields but rather one which migrated to potatoes during the drying up of other vegetation in hot, dry summers.

Yellow Top Virus

Whipple (85) reported a yellow top disease of potatoes from Montana in 1919, characterized by the upright growth habit of infected plants, yellowing and dwarfing of the apical leaves, and the production of a reduced number of small tubers. There was a tendency for the formation of additional tubers at the end of those previously formed. Spinkle-sprouts were frequent from such tubers but germination was not inhibited. Later (1926), Folsom (15, pp.20-27) in Maine described yellow top of the Green Mountain variety similar to the disease in Montana but found a leafrolling often associated with the disease. He was able to transmit the disease to healthy plants by grafting, thus demonstrated its virus nature.

In 1943 Kunkel (42) obtained diseased plants from Folsom diagnosed as infected with the yellow top virus. The virus was transmitted to potato, periwinkle, and sugar beet by means of dodder but was not transmitted by the aster leafhopper. Since sugar beet was known to be immune to aster yellows, Kunkel concluded that the yellow top virus was distinct from aster yellows.

A complete account of the yellow top virus was published in 1946 in which Folsom (17, pp.15-26) mentioned the presence of aerial tubers on infected plants as well as a net necrosis of the tubers which could be found

before harvest. He was unable to transmit the virus with aphids and found no evidence of tuber perpetuation. Folsom concluded that yellow top was probably related to the group of diseases which included eastern aster yellows, purple-top wilt, witches' broom, and apical leafroll.

Rosette Virus

Hutton and Oldaker (30) in Australia have described a disease of potatoes known as "Rosette." Symptoms include severe stunting of the plant as well as cupping and malformation of the leaves. This disease was readily transmitted to N. tabacum, tomato, and potato by grafting, which indicated that it was due to a virus. Neither sap nor aphid (Myzus persicae Sulz.) transmission was effective. Circular, hyperplastic, necrotic areas confined to the internal and external phloem were noted in diseased plants. This disease closely resembled the green dwarf reported from Oregon which is known to be caused by a strain of the curly top virus. Curly top was not known to be present in Australia.

GENERAL METHODS AND MATERIALS

Methods and materials that were used repeatedly throughout the course of these experiments will be described in this section. Any modifications or special techniques used for particular experiments will be included with those experiments.

Location of Experiments

These investigations were conducted on the Botany and Plant Pathology farm, in greenhouses at Corvallis, and in the North Unit Section of the Deschutes Project near Madras, Oregon during the period from August 1953 to March 1956.

Seed Sources and Plants Used

The virus free potatoes used in the inoculation experiments were obtained from Elmer Johnson, certification specialist at Oregon State College. Other potatoes used in these studies were obtained in the fields of the North Unit area. Seeds of the weed species used were also collected in this area. Seeds of the other species used were obtained from the Burpee Seed Company or from Dr. J. A. Milbrath. Table 1 lists the plants used in these experiments.

Virus Sources

The late-breaking virus used was obtained in the North Unit area from naturally infected potatoes which were grafted to Nicotiana rustica L., from viruliferous aster leafhoppers collected in Ladino clover fields, and from Ladino clover which manifested the phyllody typical of the late-breaking virus disease in this plant. Western aster yellows virus was obtained from Dr. J. H. Freitag at the University of California at Davis through the auspices of Dr. K. G. Swenson, entomologist at Oregon State College.

Insect Sources

Leafhoppers used in the insect transmission trials were obtained from two sources: (1) field collected leafhoppers, identified as aster leafhoppers by Mr. Clark Amen, formerly entomologist at Oregon State College, and (2) insects identified as aster leafhoppers sent from California by Dr. J. H. Freitag. Non-viruliferous insects were obtained by rearing them on barley or rye which are immune to aster yellows virus (38, p.95). The adults were removed before the eggs hatched and the colonies were tested on aster before using them for transmission trials.

Insect Manipulation Equipment

Rectangular cages (Figure 1) were used to enclose the plants used in the insect transmission trials. The

leafhoppers were transferred from plant to plant by means of a sucking tube (Figure 1) which was devised by Kunkel (35, p.649).

Insect Transmission Procedure

Plants were grown in #10 cans in a room of the plant pathology wing of the greenhouses. This room was screened against insects and was fumigated at weekly intervals with tetraethylpyrophosphate during the course of these experiments. When the plants were from three to six inches high, they were carried to the headhouse portion of the entomology wing of the greenhouses. Individual cages containing the source plant and the insects were carried from the rearing room to the headhouse and there the insects were transferred to the caged test plants. These plants were then carried to the rearing room where the insects were allowed to feed on them for a test feed period of from one day to two weeks. After removing the insects in the entomology headhouse the test plants were dusted with malathion insecticide and left in the plant pathology headhouse overnight. The test plants were then replaced in the room in the plant pathology wing. All transfers of the insects were made with a bright light at the rear of the cages so that the insects remained in the case when disturbed since they are attracted by the light. No accidental inoculation of plants occurred in any of the experiments over the

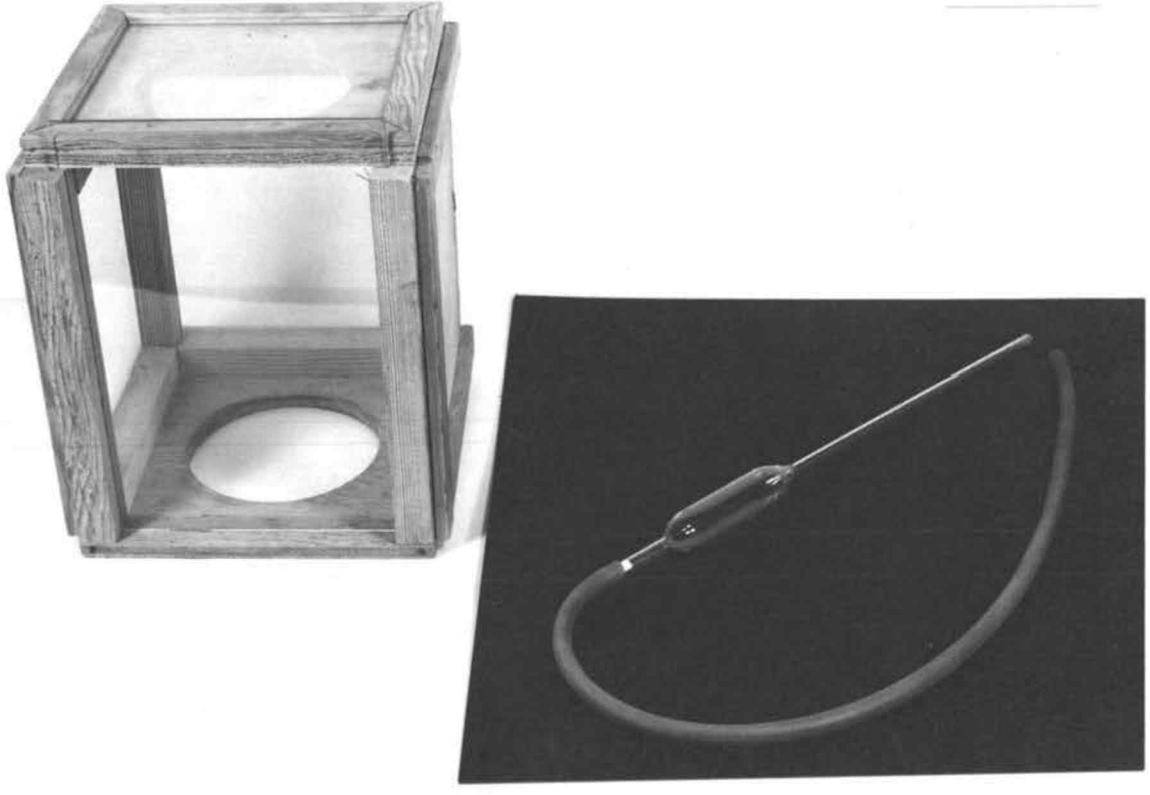

Figure 1. Insect cage and insect sucking tube.

Table 1. Plants used in experiments with the potato late-breaking virus.

Common name	Scientific name
Aster	*Calistephus chinensis* (L.) Nees
Alfalfa	*Medicago sativa* L.
Alsike Clover	*Trifolium hybridum* L.
Barley	*Hordeum vulgare* L.
Bean	*Phaseolus vulgaris* L.
Beet	*Beta vulgaris* L.
Celery	*Apium graveolens* L. var. *dulce* Pers.
Cowpea	*Vigna sinensis* Endl.
Crimson Clover	*Trifolium incarnatum* L.
Cucumber	*Cucumis sativus* L.
Dandelion	*Taraxacum officinale* Weber
Fleabane	*Erigeron canadensis* L.
Gladiolus	*Gladiolus gandavensis* Van Houtte
Jimson Weed	*Datura strammonium* L.
Ladino Clover	*Trifolium repens* L.
Lettuce	*Lactuca sativa* L. var. *capitata* L.
Lima Bean	*Phaseolus limensis* Macf.
Mullein	*Verbascum thaspus* L.
(No common name)	*Nicotiana rustica* L.
Pepper	*Capsicum frutescens* L.
Petunia	*Petunia hybrida* Vilm.
Plantain	*Plantago major* L.
Potato	*Solanum tuberosum* L.
Prickly Lettuce	*Lactuca scariola* L.
Red Clover	*Trifolium pratense* L.
Rye	*Secale cereale* L.
Scarlet Runner Bean	*Phaseolus coccineus* L.
Soybean	*Glycine max* Merr.
Squash	*Cucurbita maxima* Duch.
Squash	*Cucurbita moschata* Duch.
Tobacco	*Nicotiana tabacum* L.
Tomato	*Lycopersicon esculentum* Mill.
Zinnia	*Zinnia elegans* Jacq.

18-month period in which this greenhouse arrangement was used. The rearing room is air-conditioned and was kept at 70-80°F. during these experiments. When necessary,

additional artificial light was supplied to maintain a 15-hour light period in the rearing room. The room in the plant pathology greenhouse wing was kept at about 70° F. but on occasion reached a temperature of 90° F. for very short periods due to the lack of air-conditioning equipment.

Graft Transmission Trial Procedure

In the graft transmission experiments the following procedure was followed: In well established plants from 6" to 12" tall, depending on the species, a shallow, oblique cut was made from a point about 3/4" above a leaf axil to about 1 1/4" below this point with a razor blade. The leaf at this node was trimmed and a thin, wedge-shaped scion inserted in the cut with the cambium regions of the scion and stock matched at one edge. A leaf and bud were left on the scion in such a way that they protruded at the upper terminus of the slit in the stock. The graft was bound with Parafilm, which is a wax-like material manufactured by the Marathon Corporation, Menasha, Wisconsin. The inoculated plants were placed in a moist chamber for about six days after grafting, and then placed on the greenhouse bench. More than 90 per cent of such grafts were successful, and the scions continued growth for a reasonable period of time.

Dormancy Breaking

When potato tubers were used soon after harvest, before dormancy was naturally completed, ethylene chlorohydrin was used to break dormancy as described by Denny (13).

INSECT TRANSMISSION TRIALS

Viruses of the yellows group, with few exceptions, are not sap transmissable and under natural conditions are usually spread by insect vectors. Raymer and Amen (67) showed that the aster leafhopper might be a vector of the potato late-breaking virus. This work also indicated a close relationship between aster yellows and the late-breaking virus as well as an association of the latter virus with the phyllody condition in Ladino clover. The experiments in the following section were designed to confirm these relationships.

Comparison of Late-breaking Virus from Three Sources

When these studies were initiated the potato late-breaking virus was obtained from potato, Ladino clover, and field-collected aster leafhoppers. The aster yellows virus has been recovered from potato with an insect in only one instance (75), and that with a long-winged form of the aster leafhopper not reported from Oregon. For this reason, potatoes naturally infected with the late-breaking virus were grafted to *N. rustica* from which the aster leafhopper could acquire an aster yellows-type virus (35, p.670). Ladino clover plants with phyllody collected from fields near Madras were another source, and aster leafhoppers from the same fields served as a

third source of the late-breaking virus. A comparison of the symptoms induced in five different plant species by the viruses from these three sources is tabulated in Table 2.

Table 2. A comparison of symptoms induced by potato late-breaking virus from three sources.

Original source	Symptoms produced in				
	Aster	Potato	Ladino clover	Tomato	N. rustica
LBV Potato	AY*	LBV**	Phyllody	AY	AY
Phyllody Ladino	AY	LBV	Phyllody	AY	AY
Field-collected aster leafhoppers	AY	LBV	Phyllody	AY	AY

All inoculations were made by means of the aster leafhopper.
* AY - aster yellows virus symptoms.
** LBV - late-breaking virus symptoms.

Since the symptoms produced by the virus from each source were identical, the viruses were considered to be identical and no further distinction as to source was made. The results of these tests demonstrated:

(1) that the aster leafhopper was a vector of the late-breaking virus;

(2) that the late-breaking virus was closely related to the aster yellows virus;

(3) that Ladino clover phyllody and late-breaking of potatoes can be caused by the same virus;

(4) that tomato was susceptible to an aster yellows virus when inoculated by means of the aster leafhopper.

Host Range Tests

Although preliminary tests indicated that the late-breaking virus was closely related to the aster yellows virus, transmission of late-breaking to a legume was a point of differentiation between these two viruses. No transmission of an aster yellows virus to a legume had previously been reported. Kunkel (37) had infected tomato with the aster yellows virus by grafting but had failed to transmit the virus to tomato with the aster leafhopper. The late-breaking virus disease in potato (60) had certain characteristics differing from purple-top wilt (5, pp.25-30) caused by the aster yellows virus. For these reasons a further investigation of the identity of the late-breaking virus was necessary.

Ladino clover appeared to be the chief source of the late-breaking virus in the Madras area. Certain weed species in this area also appeared to be sources of the virus. The importance of these plants as both annual and perennial reservoirs for the late-breaking virus illustrated the desirability of further study of such hosts.

Insect transmission of the late-breaking virus to potatoes was a major problem since potatoes were infected in this manner under field conditions. Varietal susceptibility and symptom expression of potatoes infected with the late-breaking virus was an important aspect of the problem due to the similarity of the late-breaking disease to purple-top wilt.

The problems of virus identity, legume and weed hosts, and insect transmission of the late-breaking virus to potato were investigated in a series of 45 experiments (Table 3). Failures to transmit the virus to test plants were included only when the leafhoppers transmitted the virus to aster plants used as checks. The virus was recovered in aster from all plants expressing symptoms with the exception of potato. Late-breaking virus was recovered in tomato by grafting from infected potatoes. Alfalfa and Zinnia inoculated in these experiments did not express disease symptoms and the late-breaking virus was not recovered from these two species by non-viruliferous aster leafhoppers.

Table 3. Transmission of the late-breaking virus with the aster leafhopper.

Plant tested	Number infected	Per cent transmission
Aster	92/117	78.6
Alfalfa	0/12	0.0
Alsike clover	12/14	85.7
Bean	0/37	0.0
Beet	0/4	0.0
Celery	7/39	17.9
Cowpea	0/18	0.0
Crimson clover	6/6	100.0
Cucumber	0/6	0.0
Dandelion	2/5	40.0
Jimson weed	5/5	100.0
Ladino clover	18/27	66.6
Lima bean	0/8	0.0
Mullein	1/5	20.0
Nicotiana rustica	9/12	75.0
Pepper	0/7	0.0
Plantain	1/2	50.0
Potato	73/218	33.5
Prickly lettuce	11/11	100.0
Red clover	7/13	53.8
Scarlet runner bean	0/6	0.0
Squash	0/14	0.0
Sow thistle	4/5	80.0
Soybean	0/9	0.0
Tomato	11/15	73.3
Zinnia	0/6	0.0

Aster. The late-breaking virus was readily transmitted to aster plants in which were produced symptoms identical to those described by Kunkel (35) for aster yellows. Aster plants of the Azure Blue variety were used in these experiments. First indication of the disease was a clearing of the veins in young leaves followed by a general chlorosis

of the new foliage. No mottling of the leaves was observed. Normally dormant buds in the leaf axils produced elongated, chlorotic branches and the whole plant assumed an upright growth habit (Figure 2). Florets of infected flowers were stunted, green and often twisted. If very young plants, at the 5-8 leaf stage, were infected, no flowers were formed. As the age of plant prior to infection was increased, the modification of plant habit and floral structure was decreased. Aster plants infected immediately preceding flowering produced normal flowers at first but later flowers were green and malformed. First symptoms of the disease developed within 10-30 days after inoculation, depending on the age and growth rate of the plants.

Alfalfa. Both Ranger and Grimm varieties of alfalfa were tested for susceptibility to the late-breaking virus under conditions that gave 80 to 100 per cent transmission to other legumes and asters. Two separate tests were made but no disease symptoms were evident in the plants tested nor was the virus recovered from them with the aster leafhopper.

Alsike Clover. Alsike clover was tested for susceptibility to the late-breaking virus because of potential danger of the crop as a reservoir host for the virus.

this legume was readily infected with the late-breaking virus in four separate tests with plants 7-12 weeks old. Although McWhorter (54) had reported an aster yellows-like disorder of Alsike clover in the Klamath region of Oregon, no naturally infected plants of this species were found in this study. Very little Alsike was grown in the Madras area because of the extensive production of Ladino clover seed. In the Redmond area, Alsike clover was grown as a biennial so that little build-up of the late-breaking virus in these stands could be expected. Symptoms of the disease produced in Alsike clover by the late-breaking virus (Figure 3) consisted of stunting, reddening of the leaf margins, and reduction of the inflorescence to a phylloid structure. The latter was composed of many dwarfed, primary-type, green leaves on short pedicles. Some stimulation of dormant axillary buds to form inflorescences was evident.

Bean. Beans were tested for susceptibility to the late-breaking virus for two reasons: (1) plants of the Red Mexican variety with excessive axillary shoots were found in a field adjacent to potatoes with the late-breaking disease. No transmission to aster was obtained from these plants by using non-viruliferous aster leafhoppers as vectors; (2) Dana (11) reported transmission

Figure 2. Aster plant infected with the late-breaking virus.

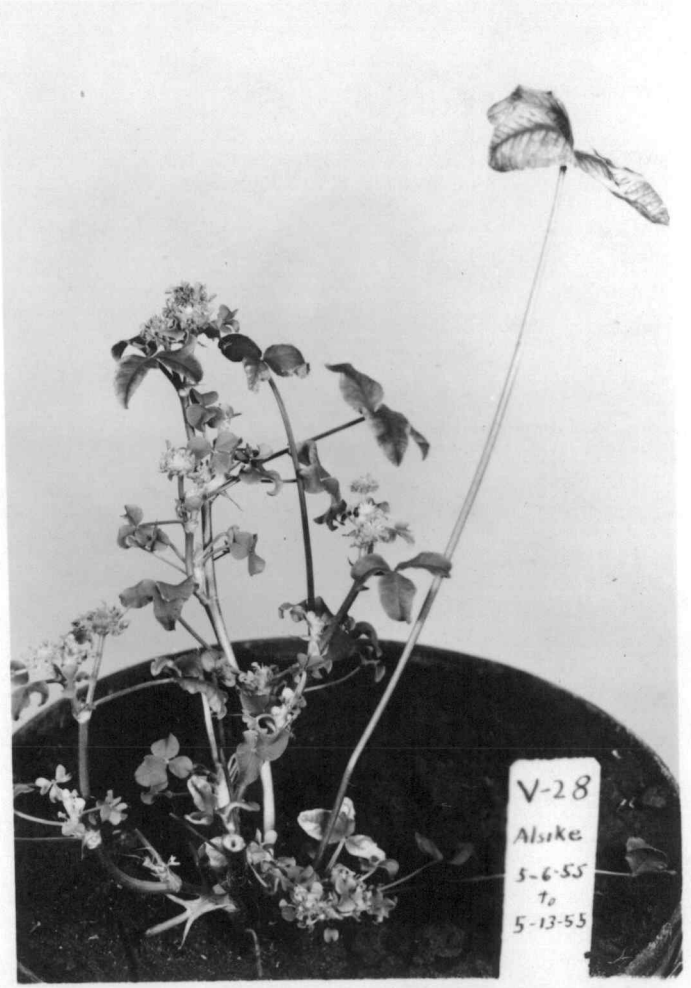

Figure 3. Alsike clover plant infected with the late-breaking virus.

of a phyllody condition in common bean by grafting. He attributed this disease to the aster yellows virus although he made no transmission to aster.

Attempts to transmit the late-breaking virus to six varieties of common beans, Red Mexican, Black Mexican, Red Kidney, Top Crop, Bountiful, and Pencil Pod Black Wax were unsuccessful.

Beet. Severin (74, p.320) and Kunkel (35, p.680) reported that beet was not susceptible to the aster yellows and in one attempt the late-breaking virus was not transmitted to this host.

Celery. Severin (74, p.322) and Kunkel (39, p.410) found celery to be the principal differential host for the eastern and western strains of aster yellows. Celery appeared to be immune from the eastern strain but quite susceptible to the western strain. Recently, Kunkel (45, p.265) was able to infect celery with the eastern strain of aster yellows by using large numbers of leafhoppers per plant to transmit the virus. The first attempts to infect celery with the late-breaking virus in Oregon were not successful. More recently, 5/5 Utah celery plants were infected with the late-breaking virus. Ten leafhoppers per plant were used as in previous experiments. A possible explanation for this erratic transmission may be that the age of celery plants was an important factor

in susceptibility. Plants grown during the winter months required a longer period of time to reach a suitable size than those grown during the spring. All celery plants were tested when they were about four inches in height. Symptoms of the late-breaking virus in celery were identical with those described by Severin (72, pp.545-550) for the western aster yellows virus. The plants were stunted (Figure 4) and chlorotic with twisted cracked petioles.

Cowpea. Two varieties of cowpea, Burpee Ramshorn Blackeye Pea and Black cowpea, were included in the host range studies. No transmission of the late-breaking virus to this species was obtained.

Crimson Clover. The late-breaking virus was transmitted to Crimson clover. In this host the virus caused a severe stunting together with a dwarfing of the leaves and reddening of the leaf margins. No inflorescences formed on the infected plants.

Cucumber. No member of the Cucurbitaceae has been shown to be susceptible to the aster yellows virus (38). Since the members of this family are susceptible to a wide range of other viruses, A and C variety, cucumber was tested for susceptibility to the late-breaking virus. Negative results were obtained.

Dandelion. Dandelion has been shown to be susceptible to the aster yellows virus (35, p.650). This perennial

weed was common on the ditch banks in the Madras area and was one of the few plants which produced foliage early in the spring before crops such as the clovers started to grow. Dandelion was infected with the late-breaking virus in these experiments. Symptoms of the late-breaking virus in dandelion closely resembled those described by Kunkel (35, p.650) for the New York aster yellows virus. Vein clearing of young leaves was followed by general chlorosis and reduction in width of the new leaves. No bronzing or reddening of the leaves was observed. Numerous new leaves from axillary buds were produced and the whole plant assumed an upright growth habit. Flowers on infected plants were green and malformed much as in aster.

Jimson Weed. Jimson weed had been considered immune from eastern aster yellows by Kunkel (38). MacLeod had been able to transmit the potato bunch-top virus to Jimson weed by grafting and dodder. Tomato big bud virus (62) was also reported to express symptoms in Jimson weed. This plant was included in the tests for susceptibility to the late-breaking virus because of its potential use as a differential host. The late-breaking virus was readily transmitted to Jimson weed by means of the aster leafhopper. First symptom of the disease in infected plants was a yellowing of the interveinal tissues of the youngest leaf followed by cessation of mesophyll development. The

Figure 4. Celery plant infected with the late-breaking virus.

Figure 5. Early stage of infection with the late-breaking virus in Jimson weed.

midrib and lateral veins continued to grow. This resulted in a retrorse curling of the leaf (Figure 5). All subsequent leaves were much dwarfed and had very short petioles. After four to five weeks a bunchy-top condition developed in the infected plants (Figure 6) due to proliferation of many dwarfed, twisted leaves on short petioles. No flowers were formed after the onset of symptom development. These symptoms somewhat resembled those due to the tomato big bud virus in this host.

Ladino Clover. In 1953 Ladino clover was extensively grown in the Madras area (Table 11) and was the principal suspect as a reservoir for the late-breaking virus. The aster leafhopper was found to be quite prevalent on Ladino clover grown for seed as well as for forage. A relatively high percentage transmission of the late-breaking virus to this species was obtained in several tests (Table 3). Symptoms induced in Ladino clover by the late-breaking virus consisted of a stunting of the plants followed by the production of phylloid inflorescences (Figure 7) as described for alsike clover. A reddening of the leaf margins was frequently associated with this disease.

Mullein. Mullein was commonly found along the roadsides and ditch banks in the Madras area. Since mullein is a perennial plant which could serve as a continual source of virus over several seasons, it was tested for

Figure 6. Late stage of infection with the late-breaking virus in Jimson weed.

Figure 7. Ladino clover plant infected with the late-breaking virus.

susceptibility to the late-breaking virus. Perhaps due to the hairy indumentum on the leaves of this species, only one plant of the five tested was infected. Symptoms of the late-breaking virus in this host consisted of extreme stunting together with dwarfing and yellowing of the new leaves (Figure 8).

Nicotiana rustica. Kunkel (35, p.685) demonstrated the susceptibility of N. rustica to the aster yellows virus, and the late-breaking virus was also transmitted to this host. Symptoms in young N. rustica plants consisted of vein clearing followed by the production of a compact cluster of stunted, twisted leaves at the apex of the stem. On older plants, long, thin shoots with narrow chlorotic leaves developed from the axillary buds (Figure 9).

Pepper. Both the tomato big bud virus (27) and the potato bunch-top virus (50) have been transmitted to pepper. No transmission of the late-breaking virus to California Wonder peppers was obtained by means of the aster leafhopper in two separate tests.

Plantain. Broad-leaved plantain was shown to be susceptible to the New York aster yellows by Kunkel (35, p.675). Plantain was prevalent along the ditch banks in the Madras area. One of the two plants tested for susceptibility to the late-breaking virus expressed disease

Figure 8. Mullein plant infected with the late-breaking virus. The plant on the right is healthy.

Figure 9. Tips of Nicotiana rustica plants infected with the late-breaking virus.

symptoms. Vein clearing in the young leaves was followed by a general chlorosis. The new foliage assumed an upright position. Small, green leaves replaced the flowers normally found in the inflorescence.

Potato. The late-breaking virus was successfully transmitted to nine varieties of potato (Table 4) by means of the aster leafhopper in tests with 218 plants (Table 3) of this species.

Table 4. Transmission of the late-breaking virus to ten potato varieties by means of the aster leafhopper.

Variety	Number infected	Per cent transmission
U.S.D.A. # 41956	0/7	0.0
Burbank	4/8	50.0
Early Gem	2/5	40.0
Irish Cobbler	2/10	20.0
Katahdin	2/10	20.0
Kennebec	6/7	85.7
Netted Gem	29/115	25.2
Pontiac	1/5	20.0
Red Pontiac	2/5	40.0
White Rose	25/46	54.3

Most of the varieties tested expressed symptoms within three weeks after inoculation. The Netted Gem variety required as long as seven weeks to express symptoms under greenhouse conditions. The low percentage transmission to this variety probably was due to maturation of the plants

before symptoms were expressed. Symptoms caused by the late-breaking virus in potatoes under greenhouse conditions resembled those found under field conditions but were much milder. First indication of infection was an upward rolling of the apical leaves. Terminal growth stopped, a reddish purple, marginal pigmentation of the upper leaflets took place, and finally tuberous swellings developed in the leaf axils (Figures 10 and 11). Pigmentation was most pronounced in the red varieties. Very few infected plants formed tubers. No necrosis of the lower stem or root was noted until the plants died. These symptoms closely resembled those described for the purple-top wilt due to the aster yellows virus (5, pp.25-30).

Prickly Lettuce. Prickly lettuce was frequently found in the Madras area with symptoms resembling those due to the aster yellows virus. This species was readily infected with the late-breaking virus. Symptoms consisted of extreme stunting, chlorosis, and dwarfing of the leaves (Figure 12). No flowers were formed on experimentally infected plants.

Red Clover. Red clover was included in the tests for susceptibility to the late-breaking virus because of its potential as a reservoir host in the Madras area where extensive plantings of the crop existed. Kenland Red clover was infected with the late-breaking virus when

Figure 10. Netted Gem potato plant infected with the late-breaking virus.

Figure 11. Irish Cobbler potato plant infected with the late-breaking virus.

inoculated by means of the aster leafhopper. Symptoms of the disease in this species resembled those produced in other clovers and consisted of stunting, dwarfing of the leaves, reddening of the leaf margins, and modification of the inflorescence to a phylloid structure. Modification of the inflorescence was less pronounced than in the case of Ladino or Alsike clover. The stunting symptom usually appeared within two weeks from the time of inoculation.

Scarlet Runner Bean. Scarlet Runner bean was included in the susceptibility tests since it does not belong to the Phaseolus vulgaris group but rather to P. coccineus and might have been a differential host. No transmission of the late-breaking virus to this species was obtained by means of the aster leafhopper.

Sow Thistle. Annual sow thistle was collected from several locations in the Madras area. Although this plant could not have acted as a source of the late-breaking virus early in the spring, it might have been a source for late season spread of the virus. Sow thistle was readily infected with the late-breaking virus in which it produced the following symptoms: stunting, chlorosis and dwarfing of the new leaves, shortening of the internodes, and inhibition of flowering (Figure 13).

Figure 12. Prickly lettuce plant infected with the late-breaking virus. The plant on the left is healthy.

Figure 13. Sow thistle plant infected with the late-breaking virus. The plant on the right is healthy.

Soybean. In the general survey of legumes for susceptibility to the late-breaking virus Bansei soybeans were tested with negative results.

Squash. Butternut and Buttercup squash varieties were tested for susceptibility to the late-breaking virus since no member of the Cucurbitaceae has been found to be a host of the aster yellows virus. No transmission of the late-breaking virus to these varieties was obtained.

Tomato. Kunkel (37) was unable to infect tomato with the New York aster yellows virus by means of the aster leafhopper although graft transmission to this host was successful. Tomato big bud virus produced enlargement of the calyx and proliferation of lateral buds in tomato (68). The late-breaking virus was transmitted to Bonny Best and Stokesdale tomatoes by means of the aster leafhopper. Symptoms of the virus in tomato were similar to those described for Jimson weed. Interveinal tissue of the youngest leaf became yellow and ceased growth, the veins continued to grow, and a narrow, retrorsely curled leaf resulted. A marked purplish color developed in the veins of these leaves. Epinasty of the older leaves was noted. Any buds or flowers present at the time symptoms were expressed in the leaves died and did not develop enlarged calyces or woody fruits. No stimulation of the axillary buds to produce excessive branches occurred. Tomatoes infected with

the late-breaking virus (Figures 14 and 15) were extremely stunted as compared with healthy plants.

Zinnia. Severin (72) demonstrated that zinnia was susceptible to the western strain of aster yellows although this species was immune from the eastern strain according to the work of Kunkel (39). In 1955 Kunkel (45, p.265) was able to infect zinnia with the eastern strain of aster yellows and thus eliminated this plant as a differential host.

The late-breaking virus was not transmitted to zinnia.

Insect Transmission of Western Aster Yellows

Western aster yellows had been transmitted to potato with the aster leafhopper (78) and produced a disease resembling the late-breaking disease. In Wisconsin (71) the western aster yellows virus had been demonstrated to be the causal agent of potato purple-top wilt in that area. Since the late-breaking virus produced symptoms of aster yellows in both aster and celery, and symptoms somewhat similar to purple-top wilt in potato, the late-breaking virus could be western aster yellows. However, no transmission of western aster yellows to clover, Jimson weed, or tomato by means of the aster leafhopper has been reported. In order to compare the late-breaking virus with western aster yellows a source of the latter virus was obtained from Dr. J. H. Freitag in California through the auspices

Figure 14. Tomato plant infected with the late-breaking virus. The plant on the left is healthy.

Figure 15. Tip of a tomato plant infected with the late-breaking virus.

of Dr. K. G. Swenson at Oregon State College. The western aster yellows virus (Table 5) and the late-breaking virus were then transmitted to a series of plants by means of the aster leafhopper in parallel experiments. Results of tests with the late-breaking virus on this series of plants are included in Table 3.

Table 5. Transmission of western aster yellows with the aster leafhopper.

Plant tested	Number infected	Per cent transmission	Symptoms
Azure Blue aster	6/6	100.0	Aster Yellows
Utah celery	5/10	50.0	Aster Yellows
Alsike clover	4/5	80.0	Phyllody
Jimson weed	3/3	100.0	Aster Yellows
Nicotiana rustica	1/2	50.0	Aster Yellows
Red Pontiac potato	1/1	100.0	Late-breaking
Burley tobacco	0/1	0.0	None
Bonny Best tomato	3/3	100.0	Aster Yellows

The symptoms on plants infected with the western aster yellows virus were identical in all cases with those produced by the late-breaking virus. These results were strong evidence that the potato late-breaking virus was identical with the western aster yellows virus. This was the first time transmission of the western aster yellows virus to a legume (Alsike clover), to Jimson weed, and to tomato had been reported.

Miscellaneous Insect Transmission Trials

Gladiolus, prickly lettuce, and Red Mexican beans with symptoms ascribed to the aster yellows virus were tested for the aster yellows virus on aster. Attempts also were made to transmit the late-breaking virus from experimentally infected potatoes to aster by means of the aster leafhopper (Table 6).

Table 6. Insect transmission to aster from several sources.

Source	Number infected	Per cent transmission	Symptoms
Red Mexican beans with excess axillary shoots.	0/4	0.0	None
Grassy top Gladiolus	3/4	75.0	Aster Yellows
Green Flower Gladiolus	2/2	100.0	Aster Yellows
Experimentally infected Netted Gem potatoes	0/2	0.0	None
Experimentally infected White Rose potatoes	0/2	0.0	None
Prickly lettuce with aster yellows symptoms	2/3	66.6	Aster Yellows

Lack of transmission from the Red Mexican beans with abnormal axillary sprouts leaves the status of this disorder in doubt. Aster yellows was obtained from Gladiolus with "grassy top" or green flowers thus confirming the work of

Smith and Brierley (80). The late-breaking virus was not acquired from potato by the aster leafhoppers used in these experiments. The disease of prickly lettuce from the Madras area which was associated with the late-breaking disease in potatoes and phyllody of Ladino clover was identified as aster yellows.

TRANSMISSION BY GRAFTING

At the inception of this study of the late-breaking virus disease of potatoes, attempts were made to secure sources of the virus. Ladino clover with phyllody was collected from the Madras area and used as a source of virus for previously non-viruliferous aster leafhoppers. These leafhoppers were fed on *N. rustica* to provide suitable material for graft transmission trials. Scions from the diseased *N. rustica* produced were grafted to several solanaceous plants and one composite, Zinnia (Table 7).

Table 7. Graft transmission of the late-breaking virus obtained from naturally infected Ladino clover.*

Plant tested	Number** infected	Per cent transmission	Symptoms
Jimson weed	7/10	70.0	Aster Yellows
Nicotiana rustica	5/8	62.5	Aster Yellows
California Wonder pepper	0/7	0.0	None
Netted Gem potato	0/8	0.0	None
White Rose potato	2/2	100.0	Late-breaking
Burley tobacco	0/8	0.0	None
Havana 38 tobacco	0/4	0.0	None
Kentucky 56 tobacco	0/5	0.0	None
John Baer tomato	0/1	0.0	None
Marglobe tomato	3/4	75.0	Aster Yellows
Blaze Zinnia	0/4	0.0	None

* The virus was transmitted from the Ladino clover to *N. rustica* by means of the aster leafhopper for use in these experiments.

** The numbers of successful grafts were used as the denominators in this category.

Later in the season when naturally infected potato plants were available in the field, N. rustica plants were infected by means of grafts from these potatoes. The late-breaking virus was then transmitted from N. rustica to potato and tomato by grafting (Table 8).

Table 8. Graft transmission of the late-breaking virus from naturally infected Netted Gem potatoes.

Plant tested	Number * infected	Per cent transmission	Symptoms
Nicotiana rustica	3/22	13.6	Aster Yellows
White Rose potato	5/9	55.5	Late-breaking
Samsun tobacco	0/2	0.0	None
John Baer tomato	2/3	66.6	Aster Yellows
Marglobe tomato	1/2	50.0	Aster Yellows
Red Cherry tomato	2/3	66.6	Aster Yellows
Rutgers tomato	4/5	80.0	Aster Yellows

* Numbers of successful grafts were used as the denominators in this category.

A comparison of the data in Tables 7 and 8 obtained with the viruses from phyllody Ladino clover and late-breaking potatoes, indicated that the virus from Ladino clover was the same as that obtained from late-breaking potatoes. Symptoms induced by graft inoculation of these plants were identical with those produced in plants inoculated by means of the aster leafhopper with the exception that

potato X virus symptoms were present in solanaceous plants inoculated from the potato source. Pepper and tobacco appeared to be immune from the virus. Although the scions on Zinnia plants produced new growth, these grafts to a non-solanaceous plant may not have been comparable with those to solanaceous plants.

TIME OF INFECTION EXPERIMENT

An experiment to determine the time of infection with the late-breaking virus under field conditions was performed in 1955. This experiment was based on the knowledge that the virus was transmitted by the aster leafhopper, and that aster was a suitable test plant for the virus. Thirty young aster plants in # 10 cans were transported to a potato field in the Madras area every two weeks from the middle of June to the first of September. These plants were placed along the west and north borders of the field at 25-foot intervals and exposed for a two-week period. At the end of each period a new set of plants was exposed and the previous set returned to Corvallis where they were dusted with malathion to kill any insects present on the plants. The aster plants were then placed in a greenhouse and dusted with malathion at weekly intervals. As symptoms developed on the asters they were recorded (Table 9) and the plants destroyed.

High incidence of disease in asters exposed in the period July 6-19, correlated well with the first appearance of late-breaking symptoms in potatoes on August first since a delay in symptom expression of 3-7 weeks after infection was known to occur in Netted Gem potatoes (60). This technique was thus a good method for the determination

of time of infection with the late-breaking virus under field conditions. This technique was not useful for determining the incidence of infection since there was no apparent correlation of the percentage of asters infected with the percentage of potatoes infected. Although 43.3 per cent of the asters during one exposure period were infected with aster yellows, only 5.5 per cent of the potatoes in this field were diseased as well as could be determined on September first.

Two periods were notable for the high incidence of aster yellows in aster plants, one in the month of July, and one in the last half of August. If these periods reflected the leafhopper populations, these results confirm Amen's (67) observations that two broods of aster leafhoppers occurred during the summer in this area. The summer of 1955 was much cooler than in the previous two years which may account for the lateness of leafhopper activity in the early summer.

Table 9. Field exposure of aster plants to determine time of infection with the late-breaking virus.

Plant position	Periods of exposure 6-16 to 7-5	7-6 to 7-19	7-20 to 8-1	8-2 to 8-15	8-16 to 9-1
West border					
1	-	AYV**	-	0	0
2	0***	-	-	0	-
3	-	-	-	-	-
4	-	-	-	-	-
5	-	-	-	-	-
6	-	AYV	-	-	-
7	-	-	AYV	-	-
8	-	-	-	0	-
9	-	-	-	-	0
10	-	-	-	-	-
11	-	-	-	-	-
12	0	AYV	-	-	-
13	-	AYV	-	-	AYV
14	-	AYV	AYV	-	-
15	-	AYV	-	-	-
North border					
16	0	-	-	-	-
17	-	-	-	-	0
18	-	-	-	-	AYV
19	0	AYV	-	-	AYV
20	0	-	-	-	-
21	-	AYV	-	-	-
22	-	AYV	-	0	0
23	0	AYV	-	-	-
24	0	AYV	0	-	-
25	-	AYV	AYV	-	0
26	-	-	-	0	-
27	-	AYV	-	-	-
28	0	-	-	-	-
29	-	-	-	-	-
30	-	-	-	-	-
Totals*	0/22	13/30	3/29	0/25	3/25
Percentage AYV*	0%	43.3%	10.3%	0%	12%

* Totals and per cent aster yellows virus were based on percentage of live plants.
** AYV - aster yellows virus.
*** 0 - plants dead.

TUBER PERPETUATION OF THE LATE-BREAKING VIRUS

Milbrath and English (60) demonstrated tuber perpetuation of the late-breaking virus for more than two generations but found such perpetuation to be very erratic from season to season. Tuber perpetuation has not been demonstrated for purple-top wilt in the eastern part of the United States (5) but was a constant feature of apical leafroll (5) in that area. These points of difference in similar diseases indicated a need for confirmation of the results with the late-breaking virus as an aid to identification of this virus. Tuber perpetuation of the late-breaking virus was also of interest because of the importance to growers of certified seed potatoes. At this time the late-breaking virus was included in the general category "total virus" for which the seed certification tolerance was 5 per cent. The tolerance for "mosaic" viruses was 2 per cent and for leafroll virus 0.5 per cent. The question existed as to whether a greater or lower tolerance for the late-breaking virus would be advisable for seed potatoes. To clarify the problems of virus identity and the importance of tuber perpetuation of the late-breaking virus, the experiments in the following section were conducted.

1953-54 Field Test

In the fall of 1953, 400 tubers from diseased plants and the same number from healthy plants were collected and stored at Corvallis. These tubers were allowed to sprout early in the spring to check for the hair sprout condition, the sprouts rubbed off, and the tubers planted in a commercial field in the Madras area. All tubers from late-breaking plants produced hair sprouts while none of the tubers from healthy plants exhibited this condition. In the field, tubers from late-breaking plants produced weak plants at first which later recovered and produced a nearly normal yield of potatoes. There was no increase of the late-breaking disease in potatoes adjacent to this plot planted with tubers from late-breaking plants.

1954-55 Field Test

In 1954 samples were again collected from healthy and diseased plants and stored through the winter. In the spring, 100 tubers from late-breaking potato plants were cut in halves longitudinally, and one-half of each tuber was allowed to sprout as a check for the hair sprout condition. Hair sprouts formed on only 42 of the 100 tubers and after sprouting these halves were held at 35° F. for later planting in the greenhouse. The other half of each tuber was held at 35° F. to prevent sprouting and then planted in the field at Corvallis. The symptoms

produced in these plants are listed in Table 10. In the field at Corvallis, current season leafroll from adjacent plantings complicated the determination of disease symptoms (Table 10). Scions from all plants with symptoms were grafted to N. rustica to test for the late-breaking virus but no transmission took place. No explanation was known for this lack of transmission.

Table 10. Incidence of symptom types in plants from 100 tubers obtained from late-breaking potatoes.

Plant symptom type	Plants from	
	Hair sprout* tubers	Non-hair sprout tubers
Late-breaking plants	3	4
Weak plants	10	9
Late-breaking ? plus leafroll plants	19	15
Healthy plants	7	17
No emergence	4	12

* Hair sprout condition was determined by allowing one-half of each tuber to sprout.

1955 Greenhouse Tests

In the fall of 1955, both tubers from all field grown plants with symptoms as well as the halves of the original parent tubers, which had been stored at 35° F. since spring,

were planted in the greenhouse. Late-breaking symptoms developed on ten potato plants from the parent tubers and on seven of the second generation plants. Grafts were made to Stokesdale tomatoes from the 17 plants with definite symptoms and from 30 additional symptomless plants selected at random to test for the late-breaking virus. Symptoms of the late-breaking virus were produced on all tomatoes inoculated from the late-breaking potatoes but not on any others.

Results

These results confirmed those of Milbrath and English (60) that the disease could be tuber perpetuated which remained as a point of distinction between the late-breaking virus and purple-top wilt. The association of the hair sprout condition with the late-breaking disease described by Milbrath and English (60, p.665) was also confirmed. Since tuber perpetuation was so erratic, no change in the certification tolerance appeared advisable. The large number of weak plants produced by tubers from late-breaking plants was sufficient justification for the existing tolerance although no spread of the disease from such plants was observed.

EFFECT OF LIGHT DURATION AND TEMPERATURE ON SYMPTOM DEVELOPMENT IN NETTED GEM POTATOES

At the outset of the transmission trials, no symptoms developed in Netted Gem potatoes experimentally inoculated with the late-breaking virus. Symptom development in plants from tubers collected in the field was likewise erratic. Tests under controlled light and temperature conditions were conducted to determine the period of light duration and temperature necessary for symptom development. In the chambers used for these experiments, temperature was controlled within a range of 2° F. and the light was of approximately 600-foot candles intensity at the plant level. Both incandescent and cool white fluorescent lamps were used to provide chromatically balanced illumination. Ten experimentally inoculated Netted Gem potato plants and five plants produced by tubers from naturally infected potatoes of the same variety were tested under each set of conditions. Five healthy check plants were included in each test. The first tests were conducted at relatively high temperatures with a long light period in an attempt to emulate field conditions during the summer. The next tests were conducted at moderate temperatures and shorter light period. The plants were shorter and had larger leaves at the lower temperatures and short light period than at the high temperatures and long light period

(Table 11). Temperatures of 65-72° F. and a light period of 11 hours appeared to be suitable for the development of symptoms of the late-breaking virus in the Netted Gem variety of potato (Figures 16 and 17).

Figure 16. Netted Gem potato plants grown at 65°F. with an 11 hour day length. The plant at the left is infected with the late-breaking virus.

Figure 17. Netted Gem potato plants grown at 72°F. with an 11 hour day length. The plant at the left is infected with the late-breaking virus.

Table 11. The effect of light duration and temperature on symptom development in Netted Gem potato plants.

Light period	Temp.	Number of plants with symptoms from: Infected tubers	Number of plants with symptoms from: Inoculated plants	Symptoms
11 hrs.	65°F.	4/5	7/10	Stunting of the plants, rolling and pigmentation of the apical leaves, aerial tubers. No normal tubers formed on infected plants. Check plants grew normally and formed small tubers.
11 hrs.	72°F.	4/5	6/10	Symptoms as for 65°F. except for some wilting of the infected plants.
15 hrs.	79°F.	0/5	0/10	All plants very tall with long internodes and small leaves. No disease symptoms were visible on any plants and no tubers were formed even on the check plants.
15 hrs.	86°F.	0/5	0/10	Plants similar to those at 79°F. but somewhat smaller, still very tall compared to those at 65 and 72°F..

FIELD OBSERVATIONS

The potato late-breaking virus disease has been rather unique as a field problem with potatoes. Most potato viruses are introduced into the field in the tubers and the control program is based primarily on the production of virus-free seed stocks. With this disease the virus apparently was coming from a source other than the potatoes which proved to be Ladino clover. Certain weeds have also been demonstrated to be susceptible to the virus but spread of the virus from these weeds could not account for the epiphytotic which occurred in 1952 and 1953. The acreages of Ladino clover in the Madras area (Table 12) have fluctuated over the ten year period since the irrigation project was completed in 1946.

Table 12. Acreages of certified Ladino clover in Jefferson County over a ten year period.

Year	Acreage	Year	Acreage
1946	279.0	1951	21,282.5
1947	673.0	1952	17,505.0
1948	1,837.5	1953	6,769.0
1949	6,324.0	1954	1,087.5
1950	16,484.0	1955	3,524.5

These data were obtained through the courtesy of Mr. Jackson Ross, extension specialist in Farm Crops at Oregon State College.

Very large acreages of this crop were grown for the three years preceding the severe outbreak of the late-breaking disease in 1952. The production in subsequent years has declined, largely due to poor prices for seed, and the incidence of the late-breaking disease has also declined. In 1953, 40 per cent of the plants in some fields of potatoes were diseased but in 1954 the highest incidence of the disease noted was 12 per cent, and in 1955 only 5 per cent. This virus was probably introduced into the Ladino clover stands from infected weeds or by leafhoppers migrating from other areas and, as the acreage of this crop increased, the reservoir of virus increased. The spring of 1952 was probably favorable for an early hatch of a large population of leafhoppers. This would allow sufficient time for the leafhoppers to feed on a source of the virus, reach the adult stage, and become infective shortly after the potatoes emerged. The Netted Gem variety of potato, which is the only variety grown commercially in this area, must be infected at an early stage if serious losses from the disease are to occur. The period during which the potatoes emerge in this area usually coincides with the time the Ladino clover is clipped in the spring which may account for the movement of the leafhoppers from the clover fields to the potatoes. The Ladino clover is an ideal over-wintering host for the

virus and a suitable breeding host for the aster leafhopper and thus represents a serious threat to the potato production in this region. The most promise for control of this disease lies in the reduction of the acreage of perennial hosts such as Ladino clover. In addition, some control may be effected by killing the leafhoppers in the clover before they can inoculate the potatoes. Perennial weed hosts should also be eliminated if possible. A dusting program in the potato fields may serve to lower the disease incidence in very severe years but will probably not prevent infection of the plants the leafhoppers first feed upon as they enter the field.

DISCUSSION

From a review of the literature on viruses which produce potato diseases similar to the late-breaking disease, the following viruses appear to be distinct: (1) apical leafroll; (2) aster yellows, which appears to be synonymous with blue-stem, late-breaking, moron, and in part with purple-top wilt and yellowtop; (3) curly top, for which rosette appears to be a synonym; (4) purple-dwarf; (5) tomato big bud, which is synonymous with purple-top wilt in Australia. The tomato big bud virus is also a component of witches' broom (89), purple-top wilt in Washington (55), and bunch-top (50). Haywire is regarded as the tuber perpetuated phase of bunch-top (50). Purple dwarf may also be related to tomato big bud although insufficient evidence of this is now available.

These viruses similar to the late-breaking virus are all of the yellows type that are not sap transmissable and are usually confined to the vascular tissue in infected plants. None have been purified nor has anti-serum been prepared for them since they are generally present at low concentrations in the plant and appear to be relatively unstable as compared with other plant viruses. As a result,

differentiation of these viruses has been based entirely on the following characteristics: mode of transmission, symptoms, and host range.

The vector of apical leafroll and the eastern strain of aster yellows is the aster leafhopper. The western strain of aster yellows is transmitted by this same insect plus 21 other leafhopper species. Curly top is transmitted by the beet leafhopper and tomato big bud in Australia by another leafhopper, Orosius argentatus. No vectors are known for witches' broom, bunch-top, purple-dwarf, or yellowtop.

In potato these viruses all produce somewhat similar symptoms of stunting, some development of axillary shoots, and often some necrosis of the vascular system. The disease syndrome produced in individual potato plants depends on the variety, time of infection, environmental conditions, and the other pathogens which might be present. Symptom development in potato plants infected with the apical leafroll virus is only slightly different from those infected with the aster yellows virus but apical leafroll is tuber perpetuated for several years with no decrease in severity of symptoms. The aster yellows and tomato big bud viruses appear to produce identical symptoms in potato. One strain of the curly top virus produces very distinctive symptoms in potato but symptoms produced by other strains

may approach those produced by the aster yellows or tomato big bud viruses. The description of purple dwarf resembles that given for tuber perpetuated symptoms of the late-breaking virus. The value of potato as a host for identification of these viruses is thus limited.

Since the interpretation of symptoms is somewhat subjective, more emphasis has been placed on host ranges of the viruses as a means of distinction. Aster yellows, curly top, and tomato big bud viruses all have extremely wide host ranges and differential hosts which are immune to one virus and susceptible to others are few in number. For example, aster yellows has not been transmitted to beet but both curly top and tomato big bud produce diseases in this host. For purposes of differentiation the pronounced differences in symptoms produced by these viruses in hosts other than potato are of more value than host range differences. The tomato big bud virus produces symptoms in tomato which are very different from those produced by the curly top or aster yellows viruses. Unfortunately, apical leafroll, yellowtop, purple dwarf, and witches' broom viruses have not been tested on a sufficient number or variety of plants to permit a direct comparison with these other viruses.

Host reactions and insect vector relationships are affected by genetic and environmental variation which

limits these characteristics as criteria of virus identification. Insect transmission of a virus has been considered to be a rather specific interrelationship between the virus and the vector species but Severin's (77) work demonstrates that more than one species of leafhopper can transmit the aster yellows virus. If this work were continued the vector of the tomato big bud virus, Orosius argentatus, might also be found to be a vector of the aster yellows virus and no further distinction between the viruses could be made on this basis. Kunkel (35) was unable to transmit a strain of the aster yellows virus to potato by means of the aster leafhopper and yet Epps (14) and others were able to transmit an aster yellows virus to potato by means of the aster leafhopper with no difficulty. This discrepancy in results may have been due to a difference in either the leafhoppers used or the viruses tested. These same alternatives are applicable to the failure of MacLeod (50) to transmit the bunch-top virus by means of the aster leafhopper. Much of the variation in symptoms on potato has been due to the use of different varieties by different workers. Test plants of other species may show the same lack of uniformity in symptom expression due to the genetic variation in plants produced from seed. In this study the late-breaking virus was transmitted to tomato by means of the aster leafhopper but Kunkel (37)

was unable to transmit a strain of the aster yellows virus to this host by means of the aster leafhopper. This difference in results may have been due to a difference in the leafhoppers, a difference in the test plant material, or a difference in the viruses involved. A difference due to the viruses alone can be determined only when the plant material and vectors used in tests with both viruses are identical. Since vectors are not known for several of these viruses, host range studies are limited to those plants which can be successfully grafted. Transmission by means of dodder has facilitated the study of host range but is also limited to those species which dodder will parasitize.

The late-breaking and western aster yellows viruses used in these studies appear to be identical. Both viruses produced identical symptoms when compared in aster, potato, N. rustica, tomato, Jimson weed, and Alsike clover plants inoculated by means of the aster leafhopper. The western aster yellows virus has not been transmitted previously to tomato, Jimson weed, and Alsike clover by means of the aster leafhopper although Kunkel (37) was able to transmit the eastern strain of aster yellows to tomato by graft inoculation. Kunkel (38) considered Jimson weed to be immune from aster yellows and was unable to demonstrate the susceptibility of any legume to this virus. In

addition to Alsike clover, the late-breaking virus has been transmitted to the following legumes: Ladino clover, Red clover, and Crimson clover.

At the present time only two strains of the aster yellows virus are distinguished (55) but there is considerable evidence for the existence of others. For example, apical leafroll differs only slightly from typical aster yellows in potato but fails to produce yellows symptoms in aster although it is transmitted by the aster leafhopper. Kunkel (35) and MacLeod (50) were unable to transmit their strains of aster yellows to potato although other workers (14, 48 and 71) have been able to transmit aster yellows viruses to this host. In contrast to the above viruses, tomato big bud, bunchtop, yellowtop, and some unidentified viruses from carrot (44) are not transmitted by the aster leafhopper but yet produce symptoms identical with those of aster yellows in many hosts. The late-breaking strain of aster yellows and the tomato big bud viruses appear to be closely related when compared on potato, Jimson weed, and the clovers. These viruses are considered to be distinct because of the difference in symptoms produced in tomato and the different vectors involved. Mutations of the aster yellows virus

have been produced (41) by heat treatment of viruliferous leafhoppers which may account for the production of strains of this virus under natural conditions.

SUMMARY

(1) The literature on ten viruses which produce symptoms in potato similar to those produced by the late-breaking virus was reviewed.

(2) The viruses obtained from late-breaking potatoes, Ladino clover with phyllody, and field-collected aster leafhoppers produced identical symptoms in aster, potato, Ladino clover, tomato, and Nicotiana rustica when these plants were inoculated by means of the aster leafhopper. The symptoms produced in potato, tomato, and N. rustica by graft inoculation with these viruses were identical with those produced by insect inoculation.

(3) The late-breaking virus was transmitted to mullein, tomato, and Jimson weed, as well as to Alsike, Red, and Crimson clovers for the first time by means of the aster leafhopper.

(4) The western aster yellows virus and the potato late-breaking virus proved to be identical when compared in aster, potato, celery, Alsike clover, Jimson weed, N. rustica, and tomato when these plants were inoculated by means of the aster leafhopper.

(5) The plant-exposure technique was shown to be a useful method for determining the period in which infection with the late-breaking virus takes place in the field.

(6) Most typical symptom development of the late-breaking virus disease in Netted Gem potatoes was produced in temperature chambers with an 11 hour day length and temperatures from 65-72° F.

(7) The incidence of the late-breaking disease in potatoes declined with the reduction in acreage of Ladino clover in Jefferson County, Oregon, from 1952 to 1955.

BIBLIOGRAPHY

1. Ashdown, D. and T. C. Watkins. Control of lettuce yellows disease in New York. Journal of economic entomology 41:252-258. 1948.

2. Black, L. M. Some properties of aster yellows virus. (Abstract) Phytopathology 33:2. 1943.

3. _____. Concepts and problems concerning purification labile insect-transmitted plant viruses. Phytopathology 45:208-216. 1955.

4. Bonde, R. and E. S. Schultz. A virus disease of the potato transmitted by aster leafhopper. (Abstract) Phytopathology 37:3. 1947.

5. _____. Purple-top wilt and similar diseases of the potato. Orono, University of Maine, 1953. 30p. (Maine. Agricultural experiment station. Bulletin no. 511)

6. Brentzel, W. E. Purple-top wilt of potato in North Dakota. Plant disease reporter 22:44-45. 1938.

7. Burke, O. D. The incidence of purple-top wilt in Pennsylvania on certain potato varieties. (Abstract) Phytopathology 31:5. 1941.

8. Conroy, R. J. Purple-top wilt of potato. Sydney, New South Wales, Department of agriculture, 1954. 12p. (New South Wales. Science bulletin no. 75)

9. Dana, B. F. Occurrence of big bud of tomato in the pacific northwest. (Abstract) Phytopathology 30:785. 1940.

10. _____. Morphological and anatomical features of phyllody in varieties of tomatoes and beans. Phytopathology 31:168-175. 1941.

11. _____. Phyllody of common beans, a graft-transmissable disease. (Abstract) Phytopathology 37:360. 1947.

12. Decker, Phares. A new potato disease in New York. Plant disease reporter 23:226-227. 1939.

13. Denny, F. E. Suggestions on inducing early germination of potato tubers in greenhouse tests for virus. American potato journal 20:171-176. 1943.

14. Epps, W. M. Purple-top wilt of potato. Doctor's thesis. Ithaca, Cornell university, 1942. (Abstracted in Review of applied mycology 24:284-285. 1945)

15. Folsom, D. Virus diseases of the potato. Report of Quebec society for the protection of plants 17:14-29. 1926.

16. _____. A celery yellows in Maine. Plant disease reporter 13:148-149. 1929.

17. _____. Potato yellow top and unmottled curly dwarf in Maine. Orono, University of Maine, 1946. 26p. (Maine. Agricultural experiment station. Bulletin 446)

18. Frazier, N. W. and E. H. Thomas. Strawberry--a host of western aster yellows virus. Plant disease reporter 37:272-275. 1953.

19. Giddings, N. J. Some studies on curly top of potatoes. (Abstract) Phytopathology 37:361. 1947.

20. _____. Two recently isolated strains of curly-top virus. Phytopathology 44:123-125. 1954.

21. _____. Some studies of curly-top on potatoes. Phytopathology 44:125-128. 1954.

22. Giddings, N. J., C. W. Bennett and A. L. Harrison. A tomato disease resembling curly-top. Phytopathology 41:415-417. 1951.

23. Goldin, M. I. and A. P. Parieuskaya. Woodiness of tomatoes in the Crimea. Microbiology 19: 527-531. 1950.

24. Goss, R. W. A review of the disease problems confronting the Nebraska growers of seed potatoes. In Report of the Nebraska potato improvement association, Lincoln, Nebraska, 1936. 14p.

25. Hervey, G. E. R. and W. T. Schroeder. The yellows disease of carrot. Geneva, 1949. 29p. (New York. Agricultural experiment station. Bulletin no. 737)

26. Hill, A. V. Big bud of tobacco. Journal of the council for scientific research of Australia 10:309-312. 1937.

27. _____. Insect transmission and host plants of virescence (big bud) of tomato. Journal of the council for scientific and industrial research of Australia 16:85-90. 1943.

28. Hill, A. V. and G. A. Helson. Distribution in Australia of three virus diseases and of their common vector Orosius argentatus (Evans). Journal of the Australian institute of agricultural science 15:160-161. 1949.

29. Hill, A. V. and M. Mandryk. A study of the virus diseases big bud of tomato and yellow dwarf of tobacco. Australian journal of agricultural research 5:617-625. 1954.

30. Hutton, E. M. and C. E. W. Oldaker. Rosette, a virus disease of the potato in Tasmania. Journal of Australian agricultural science 15:25-30. 1949.

31. Jensen, D. D. and H. Earl Thomas. Transmission of the green valley strain of cherry buckskin virus by means of leafhoppers. (Abstract) Phytopathology 45:694. 1955.

32. Jensen, J. H. and H. G. Tate. Aster-yellows and its vectors on potatoes in Nebraska. Phytopathology 37:69-71. 1947.

33. Jones, L. K., C. L. Vincent and E. F. Burk. The resistance of progeny of Katahdin potatoes to viruses. Journal of agricultural research 60: 631-644. 1940.

34. Kunkel, L. O. Insect transmission of aster-yellows. (Abstract) Phytopathology 14:54. 1924.

35. _____. Studies on aster-yellows. American journal of botany 13:646-705. 1926.

36. _____. Further studies on aster yellows. (Abstract) Phytopathology 18:156. 1928.

37. _____. Transmission of aster yellows to tomato. (Abstract) Phytopathology 20:129. 1930.

38. _____. Studies on aster yellows in some new host plants. Contributions from the Boyce Thompson institute for plant research 3:85: 123. 1931.

39. _____. Celery yellows of California not identical with the aster yellows of New York. Contributions from the Boyce Thompson institute for plant research 4:405-414. 1932.

40. _____. Effect of heat on the ability of Cicadula sexnotata (Fall.) to transmit aster yellows. American journal of botany 24:316-327. 1937.

41. _____. Isolation of mild strains of aster yellows from heat-treated leafhoppers. Journal of bacteriology 34:132. 1937.

42. _____. Potato witches' broom transmission by dodder and cure by heat. Proceedings of the American philosophical society 86:470-475. 1943.

43. _____. A new yellows disease of carrots. Journal of bacteriology 50:238. 1945.

44. _____. Identification of bolting disease of carrots. (Abstract) Phytopathology 41:22. 1951.

45. _____. Cross-protection between strains of yellows-type viruses. Advances in virus research 3:251-273. 1955.

46. Lackey, C. F. Histological studies of a tomato disease resembling curly-top. Phytopathology 41:418-419. 1951.

47. Leach, J. G. Further experiments on the cause of purple-top wilt of potatoes. (Abstract) Phytopathology 29:14. 1939.

48. Leach, J. G. and G. F. Bishop. Purple-top wilt (blue stem) of potatoes. Morgantown, West Virginia university, 1946. 35p. (West Virginia. Agricultural experiment station. Bulletin No. 326)

49. Long, H. D. Purple-top disease linked with hair-sprout tubers. In Iowa state horticultural society report no. 70. Ames, Iowa state college of agriculture and mechanic arts, 1935. pp. 314-316.

50. MacLeod, D. J. Studies on the bunch-top (purple-top wilt) disease of potatoes. (Abstract) Proceedings of the Canadian phytopathological society 16: 14-15. 1949.

51. _____. Aster yellows (purple-top) of potatoes. American potato journal 31:119-128. 1954.

52. Maramorosch, K. Multiplication of plant viruses in insect vectors. Advances in virus research 3:221-248. 1955.

53. McKay, M. B. and T. P. Dykstra. Sugar-beet curly-top virus, the cause of western tomato blight. (Abstract) Phytopathology 17:39. 1927.

54. McWhorter, Frank P. Natural occurrence of aster yellows? on Trifolium hybridum. Plant disease reporter 34:322. 1950.

55. Menzies, J. D. Purple-top virus of potatoes in Washington. (Abstract) Phytopathology 40: 968. 1950.

56. _____, Pathologist. Irrigation experiment station, Prosser, Washington. December 2, 1955.

57. Menzies, J. D. and N. J. Giddings. Identity of potato curly-top and green dwarf. Phytopathology 43: 684-686. 1953.

58. Michailowa, P. V. Pathologico-anatomical changes in the tomato incident to development of woodiness of the fruit. Phytopathology 25:539-558. 1935.

59. Milbrath, J. A. Green dwarf: a virus disease of potato. Phytopathology 36:671-674. 1946.

60. Milbrath, J. A. and W. H. English. A late-breaking virus disease of potatoes. Phytopathology 39: 463-469. 1949.

61. Muncie, J. H. Occurrence of bacterial rat and purple-top wilt of potatoes. Plant disease reporter 24:6-7. 1940.

62. Norris, D. O. Purple-top wilt, a disease of potato caused by tomato big bud virus. Australian journal of agricultural research 55:153-157. 1937.

63. Orton, C. R. and L. M. Hill. An undescribed potato disease in West Virginia. American journal of agricultural research 55:153-157. 1937.

64. _____. Further observations on blue-stem of potato. American potato journal 15:72-77. 1938.

65. Orton, C. R. and J. G. Leach. In plant pathology investigation in the United States. Plant disease reporter, supplement 191-36-118. 1950.

66. Panjan, T. Investigations into "stolbur" of the Solanaceae and a method of control. (Abstract) Review of applied mycology 51:438. 1950.

67. Raymer, W. B. and Clark R. Amen. Association of late-breaking virus in potato with a phyllody condition in Ladino clover. (Abstract) Phytopathology 44:503. 1954.

68. Samuel, G., J. G. Bald and C. M. Eardley. "Big-bud," a virus disease of the tomato. Phytopathology 23:641-653. 1933.

69. Sanford, G. B. and S. B. Clay. Purple dwarf, an undescribed potato disease in Alberta. Canadian journal of research (Section C) 19:68-74. 1941.

70. Schultz, E. S. and R. Bonde. Apical leafroll of potato. Phytopathology 19:82-83. 1929.

71. Self, R. L. and H. M. Darling. Purple-top disease of the potato in Wisconsin. Madison, University of Wisconsin, 1953. 23p. (Wisconsin. University. Research bulletin no. 184)

72. Severin, H. H. P. Yellows disease of celery, lettuce, and other plants transmitted by Cicadula sexnotata (Fall.). Hilgardia 3:543-571. 1929.

73. _____. Additional host plants of curly-top. Hilgardia 3:595-629.

74. _____. Experiments with aster yellows virus from several states. Hilgardia 8:305-325. 1934.

75. _____. Potato naturally infected with California aster yellows. Phytopathology 30: 1049-1051. 1940.

76. _____. Evidence of non-specific transmission of California aster yellows virus by leafhoppers. Hilgardia 17:21-59. 1945.

77. _____. Newly discovered leafhopper vectors of California aster yellows virus. (Abstract) Phytopathology 37:364. 1947.

78. Severin, H. H. P. and Frank A. Haasis. Transmission of California aster yellows to potato by Cicadula divisa. Hilgardia 8:327-335. 1934.

79. Severin, H. H. P. and Julius H. F. Freitag. Ornamental flowering plants naturally infected with curly-top and aster yellows viruses. Hilgardia 8: 233-262. 1934.

80. Smith, F. F. and P. Brierley. Yellows in shallot and gladiolus. Phytopathology 38:581-583. 1948.

81. _____. Aster yellows in canna. Phytopathology 41:190-191. 1951.

82. Smith, R. E. Growing China asters. Hatch, Massachusetts agricultural college, 1902. 26p. (Massachusetts. Experiment station. Bulletin no. 79)

83. Tervet, I. W. Purple-top wilt of potato and the aster yellows virus in the Dakotas. Plant disease reporter 28:816-817. 1944.

84. Webb, R. E. and E. S. Schultz. Ladino clover--a possible source of the virus causing purple-top wilt in potato. Plant disease reporter 39-300-301. 1955.

85. Wipple, O. B. Degeneration in potatoes. Bozeman, Montana state college, 1919. 15p. (Montana. Agricultural experiment station. Bulletin no. 130)

86. Wright, N. S. Witches' broom of potato in British Columbia. (Abstract) Proceedings of the Canadian phytopathological society 17:11. 1950.

87. _____. Thirty-first annual report of the Canadian plant disease survey, 1951. Ottawa, Canada, Department of agriculture, Experimental farm branch, 1951. 72p.

88. _____. Thirty-second annual report of the Canadian plant disease survey, 1952. Ottawa, Canada. Department of agriculture, Experimental farm branch, 1952. 68p.

89. _____. Studies on the witches' broom virus disease of potatoes in British Columbia. Canadian journal of botany 30:735-742. 1952.

90. _____. The witches' broom virus disease of potatoes. American potato journal 31:159-164. 1954.

91. Young, P. A. Transmission of potato witches' broom to tomatoes and potatoes. Science, N. S., 47:304-306. 1929.

92. Younkin, S. G. Purple-top wilt of potatoes caused by the aster yellows virus. American potato journal 20:177-183. 1943.