

Sources and Dissemination of Potato Viruses in the Columbia Basin of the Northwestern United States

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ABSTRACT

Thomas, P. E. 1983. Sources and dissemination of potato viruses in the Columbia Basin of the northwestern United States. *Plant Disease* 67:744-747.

The incidence of efficiently aphid-transmitted potato leafroll virus (PLRV) and potato virus Y (PVY) increased 1,600 and 2,000%, respectively, during the growing season in potato fields of the Columbia Basin, whereas the incidence of viruses more dependent upon mechanical transmission, potato viruses X (PVX) and S (PVS), increased only 600 and 350%, respectively. Volunteer potato plants were implicated as the chief sources of virus vectors and of inoculum, accounting for the increases in incidence of PLRV and PVY. The volunteers arose from tubers missed during harvest of the previous year, often growing profusely in fields planted to wheat or corn following potatoes in the cropping rotation and had the same virus incidence as fall-harvested tubers. Large numbers of aphids were present on volunteers in wheat and cornfields but not in potato fields by mid-June. Yet, an abrupt increase in PLRV infection began 5 or 6 wk later, a period equal to the incubation period for PLRV in mature potato plants. Only a massive influx of viruliferous aphids supplied through the midsummer aphid migration that characteristically occurs in the Columbia Basin could account for such an increase in PLRV infection, and volunteer plants in neighboring grain fields were the only outside source of aphids and virus. Most PLRV infection was concentrated in a few fields and data indicate the difference between good and poor control may be attributable to a single management practice. The midsummer influx of vectors was also necessary for the increase in PVY infection, but seed tubers may have been a more important source of inoculum for PVY. Most seed lots were totally infected or had about 50% PVS, but a few were PVS-free. Most seed lots were free of PVX or had about 25% PVX, but a few were totally PVX-infected.

About 20% of the potatoes grown in the United States are grown in the Columbia Basin region of the Northwest (12). Surveys conducted there by Powell and Mondor (6) in the late 1960s showed that more than 40% of the tubers harvested were infected with potato leafroll virus (PLRV). Other reports concerning occurrence of potato viruses in potato fields of the Columbia Basin are lacking.

The objectives of these studies were to survey potato fields of the Columbia Basin for the major potato virus diseases, to determine the primary sources of virus inocula, and to determine the means of virus dissemination from sources to the growing potato crop.

Potato viruses overwinter in tubers missed in the previous harvest (3), and volunteer plants emerging from such tubers have been implicated as a primary source of inoculum in the epidemiology

of potato viruses in many regions of the world (11). Because volunteers were observed growing profusely in many fields of the Columbia Basin, it seemed possible that they were a major source of inoculum for the potato virus diseases that occur there.

Because of the high aphid populations in the Columbia Basin (6), even low incidence of seed infection could be very important in the epidemiology of potato viruses. Thus, seed tubers were investigated as a second potential source of virus inoculum. Seed infection eliminates the requirement for movement of viruses from outside sources into the potato field. This movement is a particularly difficult step in dissemination of viruses transmitted by contact, by soil-inhabiting agents, and by insects in a nonpersistent manner.

There are few domestic plants in the Columbia Basin that could serve as sources of potato virus inoculum because the potato-growing regions are sparsely populated. Only annual weeds occur in potato fields, and the native desert flora there could not provide a source of primary inoculum because it is dry or dormant during the period of potato virus dissemination. Thus, these plants were not investigated as potential sources of inocula.

MATERIALS AND METHODS

Virus disease survey. Fifty tubers were collected early in September from each of

70 fields in the Columbia Basin. The fields were selected to represent the entire Basin and samples were taken at locations to represent all areas of each field. The tubers were stored at 4 C until March, when two plants were grown from each tuber in a glass greenhouse in a soilbed deficient in nitrogen (to intensify PLRV symptoms) at 24–28 C. Each plant was then indexed for potato viruses A, M, S, X, Y, and PLRV. Visual symptoms in the young plants were used to identify PLRV infections and reliability of symptoms was verified by aphid transmissions from the young plants to the PLRV indicator host, *Physalis floridana* L. (14). Viruses S, X, and Y were identified serologically in the young plants by radial immunodiffusion (7). These viruses, along with viruses A and M, were further identified by symptoms after mechanical inoculation on the diagnostic hosts *Gomphrena globosa* L., *Nicotiana tabacum* L. 'Xanthi-nc,' *N. debneyi* L., *Phaseolus vulgaris* L. 'Red Kidney,' and *Datura tatula* L. (3) and on two selections of *Solanum demissum* PI 175404 and PI 23059 selected as diagnostic hosts for potato viruses A and Y, respectively (13,15).

Virus content of seed potatoes. Incidence of virus infection was determined in each of the seed potato samples submitted to the 1979 Washington Foundation Seed Trials. These samples represented seed lots under increase by growers and destined to be sold in the Columbia Basin as commercial seed potatoes for the next season. A 3-cm-long section of the growing end of each of 48 randomly selected tubers in each seed lot was planted in a screenhouse in May. The young plants were inspected visually for symptoms and individually analyzed by enzyme-linked immunosorbent assay (ELISA) (4) for potato viruses S, X, Y, and PLRV. In addition, the field readings for each seed lot, made by the Washington State Department of Agriculture, were noted.

Overwinter survival of viruses in tubers in the field. Incidence of viruses S, X, Y, and PLRV in fall-harvested tubers was compared with incidence of the same viruses in volunteer potato plants growing in the same experimental plots the following spring. Ten tubers were collected in each of three replicates of five 0.1-ha treatment subplots of a plot seeded to winter wheat after potato harvest. Similar collections were made in subplots

This research was supported in part by grants from the Washington State Potato Commission.

Accepted for publication 4 January 1983.

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that remained fallow over the winter. The five subplot treatments applied primarily to determine their effects on growth of volunteers were: 1) untreated control, 2) telone C-17 (1,3-dichloropropene [76.3%] and chloropicrin [17.1%]) injected 23 cm deep with shanks 23 cm apart at 1.12 kg/ha on 3 October, 3) the same telone treatment injected on 20 March, 4) maleic hydrazide (Royal-MH-30, 21.7% potassium salt of 1,3-dihydro-3,6 pyridazineione) applied as a foliage spray at 3.4 kg a.i./ha in 150 L of water containing 250 ml of nonionic detergent at 2 wk after full bloom, and 5) the same maleic hydrazide treatment applied 4 wk after full bloom.

The tubers were held at 4 C over the winter and planted in a screenhouse in May. Young plants growing from the tubers were inspected visually for symptoms and assayed for virus content by ELISA. Young volunteer plants collected from the same plots were inspected visually and analyzed for virus content.

Aphid populations on volunteer potato plants and in commercial fields. Aphid populations on volunteer potato plants were determined on 15 June on the same experimental plots used to determine the survival of viruses overwintering in the tubers. A leaflet near the soil line was taken from 10 plants in each of the treatment subplots and held in a petri plate until the aphids on each 10-leaflet sample were counted in the laboratory. Concurrently, aphid counts were made from 50-leaflet samples collected in each of 28 commercial potato fields throughout the Columbia Basin. These were the same fields used to determine rate of local virus dissemination.

Virus dissemination during growing season. Twenty-eight Russet Burbank potato fields representing all areas of the Columbia Basin were selected. At weekly intervals throughout the growing season, 50 randomly selected plants in each field were inspected for PVY-type symptoms and a leaf sample from each plant was analyzed for PLRV infection by the IKI starch staining method (10).

RESULTS

Extent of virus dissemination. Incidence of virus infection in tubers used as seed in the Columbia Basin (Table 1) was relatively low compared with that in tubers harvested in the fall (Table 2). Of 403 seed lots in the 1977 Washington Seed Lot Trials, only 20 lots contained one or more plants with PLRV symptoms and the highest incidence was about 5%. Mosaic symptoms occurred in only 37 of the seed lots, with the highest incidence about 4%. Results of clinical diagnosis (Table 1) indicated that incidence of virus infection in the seed tubers submitted for the seed lot trials was somewhat higher than the field readings indicated.

In contrast, over 90% of the tubers

Table 1. Incidence of virus infection in seed tubers of the 1979 Voluntary Washington Foundation Seed Lot trials

Virus	No. of seed lots			Infection (%)		
	Tested ^a	Not infected	100% infected	Range	Average ^b	Average ^c
Potato leafroll virus	73	46	0	0-13	2.2	6.0
Potato virus S	77	13	48	0-100	23.2	52.0
Potato virus X	77	32	14	0-100	12.9	26.0
Potato virus Y	77	43	0	0-13	0.64	1.7

^a A young plant grown from each of 48 tubers from each seed lot was tested individually in one replicate by ELISA.

^b Average percent tubers infected among partially infected plus virus-free seed lots.

^c Average percent tubers infected among partially infected seed lots.

Table 2. Incidence of virus infection in 70 Columbia Basin potato fields at harvest^a

Virus	Means of diagnosis	Infection (%)	
		Range	Average
Potato leafroll	Symptoms	0-90	37
Potato virus A	Diagnostic host ^b	...	0
Potato virus M	Diagnostic host ^c	0-74	32
Potato virus Y	Serology	0-42	13
Potato virus X	Diagnostic host ^d	6-100	75
Potato virus S	Serology	8-100	78
Tobacco rattle	Symptoms	...	0

^a Two young plants grown from 50 tubers collected from each of 70 fields in the fall near harvest time were individually diagnosed.

^b *Solanum demissum* PI 175404.

^c *Phaseolus vulgaris* 'Red Kidney.'

^d *Gomphrena globosa*.

Table 3. Survival of potato viruses in tubers remaining in the field over the winter and emerging as volunteer plants in the spring

Virus	Incidence of Infection ²	
	Fall tubers	Volunteer plants
Potato leafroll	68 a	60 a
Potato virus Y	40 b	41 b
Potato virus X	11 c	13 c
Potato virus S	100 d	100 d

² Each number is the mean percentage infection in three replicate 10-plant samples from each of 15 plots. Means followed by different letters are different ($P=0.05$).

harvested from 70 fields in the Columbia Basin were infected by one or more viruses (Table 2). Incidence was 20 times greater for PVY, 16 times greater for PLRV, 6 times greater for PVX, and 3.5 times greater for PVS (based on clinical diagnosis of Seed Lot Trials) in harvested tubers than in the seed tubers.

Of 77 seed lots tested, 48 were totally infected with PVS, 16 were partially infected at an average incidence of 52%, and 13 were free of PVS (Table 1). Only 14 seed lots were totally infected with PVX, 31 were partially infected at an average incidence of 26%, and 32 were free of PVX. No commercial fields were free of either latent virus at harvest (Table 2). Incidence of infection in fields less than totally infected at harvest ranged from 8 to 78%, and from 6 to 66% for PVS and PVX, respectively.

Overwinter survival of viruses in tubers in the field. There were no differences in incidence of virus infection between fall-

Table 4. Numbers of aphids on volunteer potato plants on 15 June

Treatment	No. of aphids ^w	
	Wheat cover crop	No cover crop
Maleic hydrazide 30 + 2 wk ^x	2.3 a	18.7 b
Maleic hydrazide 30 + 4 wk ^x	1.7 a	14.3 b
Control	1.7 a	12.3 b
Telone C-17, 3 October ^y	1.7 a	11.7 b
Telone C-17, 20 March ^y	1.3 a	10.7 b
Means ^z	1.7 a	13.5 b

^w Each number is the mean number of aphids on three replicate samples of 10 leaflets. Each sample was taken from a different 0.5-ha plot and each leaflet was taken from a different volunteer plant near the soil line.

^x Number of weeks after full bloom.

^y Application date.

^z Means in columns or rows followed by the same letter are not significantly different ($P=0.01$).

harvested tubers and volunteer potato plants collected from the same experimental plots (Table 3). Because fumigating the soil with telone C-17, growing winter wheat after potatoes, and treating potato foliage with maleic hydrazide all reduce numbers of volunteers (9), it seemed possible that these treatments might have a greater effect on tubers already weakened by virus infection than on healthy tubers. None of these treatments, however, changed the incidence of infection in volunteers from that in fall-harvested tubers or from that in

volunteers growing in untreated control plots.

Aphid populations on volunteer potato plants and in commercial potato fields. Although many aphids were present on volunteer potato plants in wheat plots by 15 June, nearly eight times as many were present on volunteers in corresponding fallow plots (Table 4). Neither maleic hydrazide nor telone C-17 affected numbers of aphids per leaflet on volunteer plants. Volunteer plants in the

fallow plots were shorter, greener, and had larger leaflets than those in wheat plots, but the number of leaflets per plant was about the same as on those in the wheat plots. In commercial fields, volunteer potato plants in cornfields were more robust than those in wheat fields.

One or more aphids were found in only seven of 28 commercial potato fields sampled on 15 June. Four fields had one aphid, two had two aphids, and one had five. The fields in which aphids were

found early in the season ranked among the highest in PLRV incidence at the end of the season.

Local virus dissemination. Incidence of PLRV among plants in the 28 fields selected to monitor the seasonal pattern of virus dissemination was about 4% in the initial sampling on 1 June based on diagnostic tests (Fig. 1). Incidence remained nearly constant through mid-July, then increased rapidly to 30% at the last sampling on 17 August; however, only 7.5% of these plants had symptoms of PLRV on 17 August and 1.5% had PVY-type symptoms. Based on symptoms on plants grown from tubers harvested from plants sampled on 17 August, 34% were infected with PLRV.

At the final reading, most of the 28 fields monitored had either a relatively high or a low virus incidence (Fig. 2). The high-incidence category peaked in the 60-69 percentile range, which contained 21% of the fields and 44% of the infected plants in the 28 fields. Fourteen fields with the highest incidence contained 89% of the PLRV-infected plants, and the mean increase in incidence of PLRV in these fields was 25-fold. In the low-incidence category, the 0-9 percentile range contained 32% of the fields but only 3.6% of the infected plants.

DISCUSSION

Incidence of virus infection was much higher in tubers harvested from Columbia Basin fields than in those used as seed to grow the crop. The increase in incidence during the growing season was much greater for the viruses that are efficiently aphid-transmitted, like PLRV (1,600% increase) and PVY (2,000% increase), than for those that are more dependent on mechanical transmission like PVX (600% increase) and PVS (350% increase) (5).

Volunteer potato plants were implicated as the chief source of both the primary virus inoculum and the aphid vectors associated with dissemination of potato viruses in the Columbia Basin. Volunteers grow profusely in wheat and cornfields that normally follow potatoes in the cropping rotations, and incidence of viruses in the volunteers was the same as in tubers produced in the previous year's crop, regardless of treatments or cropping practices used to prevent or retard growth of volunteers. Although chemical and cultural treatments affected numbers of volunteers (9), the virus content of volunteers reflects the previous year's virus disease incidence. Furthermore, populations of aphid vectors built up early in the season on the volunteer plants.

In contrast to the large aphid populations on volunteer plants, there were essentially no aphids in potato fields as late as 14 June. Yet, a rapid increase in incidence of PLRV began in late July and early August. Only a massive influx of

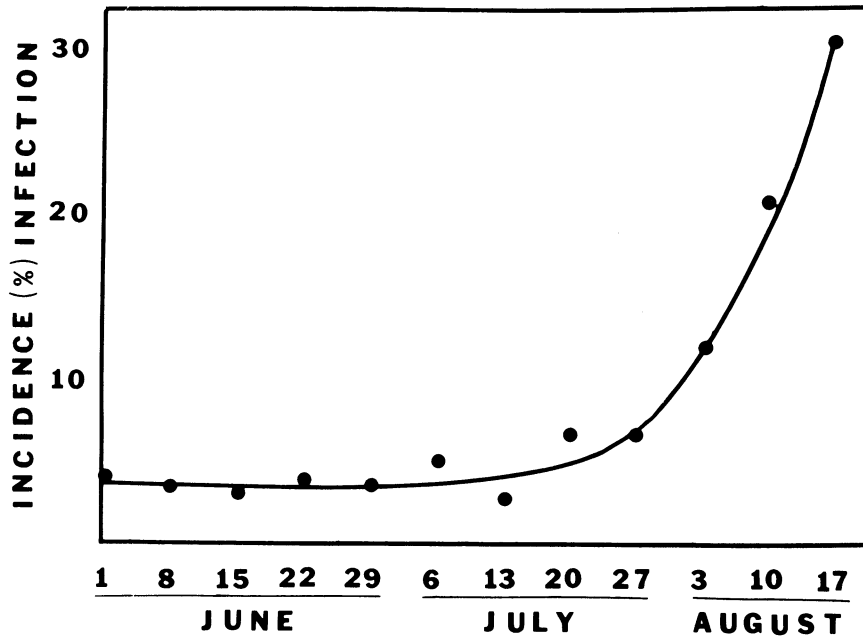


Fig. 1. Mean incidence of potato leafroll virus infection in 28 Columbia Basin potato fields in weekly intervals throughout the growing season.

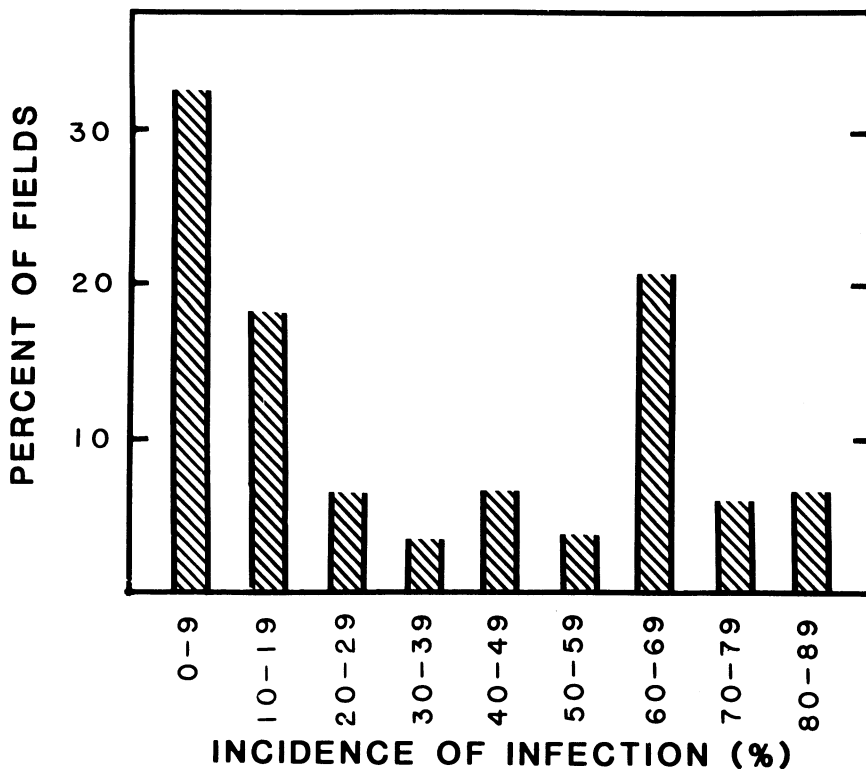


Fig. 2. Percentile distribution of 28 Columbia Basin potato fields according to incidence of infection with potato leafroll virus.

viruliferous aphids from outside sources could account for such an increase, and the influx would need to occur soon after the 14 June aphid counts because a 5- to 6-wk incubation period is required after inoculation at midseason for detection of PLRV (10). Powell and Mondor (6) described a major aphid migration in the Columbia Basin that characteristically begins in mid-June. Such a migration could account for the large influx of viruliferous aphids into potato fields originating from the volunteer plants in wheat and corn fields.

Much potential primary inoculum was present in the seed tubers planted in the Columbia Basin, but data indicate this inoculum played a minor role in PLRV epidemiology. Because of the long incubation period for PLRV and PVY in mature plants (2,10), all the infection detected at the end of the season must have been initiated within 3 wk after the 14 June aphid counts, and none could have resulted from secondary dissemination from plants infected with primary inoculum. Because aphids were not present in potato fields on 14 June, the aphids required for any intrafield dissemination necessarily originated from an outside source via the midsummer aphid migration (6). A 25-fold increase in incidence of PLRV occurred in 50% of the fields with the highest infection. An increase of this magnitude based on intrafield dissemination would require that the equivalent of five migrating aphids land on each infection source, acquire the virus, and transmit it to five other plants. In contrast, the same increase would be achieved if but one in 500 of the same population of migrating aphids carried the virus and transmitted it to five plants.

In contrast to PLRV, intrafield dissemination of primary inoculum derived from seed tubers appears to play a major role in the epidemiology of PVY in Columbia Basin potato fields. Because PVY is a styletborne virus, aphids migrating into potato fields could lose PVY infectivity before arriving. Furthermore, it is probable that secondary dissemination of PVY does not occur because dissemination does not begin until the aphids arrive in mid-June, and systemic virus invasion of mature potato

plants by PVY is even slower than it is by PLRV (1). Increase in virus incidence, however, was greater for PVY than for PLRV. Its rate of dissemination from local sources is favored because it is styletborne. In addition, the mid-June aphid migration occurs at a time when the residual level of the systemic insecticides applied in the soil at plant emergence is falling below that required to kill aphids (D. M. Powell, *personal communication*). Under these conditions, aphids may live for some time and the systemic insecticides actually stimulate rate of virus transmission (8), especially of styletborne viruses like PVY, by affecting feeding behavior and movement of the vector.

The failure of aphid populations to build up before 14 June in any of the 28 commercial potato fields monitored while large populations built up on volunteer potato plants is explicable on the basis of nearly universal usage of persistent systemic insecticides applied to the soil at plant emergence in the Columbia Basin. The insecticide apparently kills the nonviruliferous aphids initially dispersed from peach trees in the spring. Because little aphid movement occurs after that until the midsummer migration (10), little or no aphid-mediated virus dissemination occurs in commercial potato fields in early summer.

The fact that one-third of the potato fields studied in the Columbia Basin had less than 10% incidence of PLRV at the end of the growing season indicates that effective virus disease control is routinely achievable under proper management. The fact that most fields had either a relatively high or low incidence of infection indicates that the difference between efficient and inefficient control may be attributable largely to a single management practice. The data indicate this practice involves control of either volunteer potato plants or the dissemination of virus from those plants to the new crop after mid-June.

Results involving the latent, largely mechanically transmitted viruses indicate that most seed growers supplying the Columbia Basin make little or no effort to control PVS. Of 77 seed lots, 64 were either totally infected or infected at an average incidence of 52%. The fact that 29

seed lots were less than totally infected indicates that these lots originated from PVS-free nuclear stocks. The fact that 13 seed lots were free of PVS suggests that reinfection can be prevented under proper management. Growers are controlling PVX more successfully than PVS. Nearly four times as many more seed lots were totally PVS- as PVX-infected, 2.5 times as many were free of PVX than of PVS, and twice as many tubers were PVS-as PVX-infected in partially infected seed lots.

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