Beet Western Yellows Virus—A Major Component of Some Potato Leaf Roll-Affected Plants

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ABSTRACT

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Beet western yellows virus (BWYV) has been isolated from potato stocks with typical potato leaf roll (PLR) symptoms. Virus isolates from potato, that induce leaf rolling, interveinal chlorosis, petiole epinasty, and reduction in leaf size in *Physalis floridana* and interveinal chlorosis on *Capsella bursa-pastoris* have been shown to be strains of BWYV. Isolates differing in host reaction and serological characteristics have been found in individual potato plants indicating a complex etiology for the PLR syndrome. In addition to potato, and other solanaceous hosts, one isolate has been transmitted to and recovered from species in the Boraginaceae, Chenopodiaceae, Compositae, Cruciferae, Leguminosae, Malvaceae, and the Portulaceae. The BWYV isolates induce primary leaf roll symptoms in PLRV-free and virus-free potato cultivars, indicating that these isolates might easily be confused with "typical" PLRV. Preliminary serological data indicate that there are several serotypes of BWYV in potato that differ from each other and from PLRV in serological reactions. This evidence suggests that serological testing for PLRV occurrence would probably give misleading information. The broad host range of these BWYV isolates raises questions about the reinfection of virus-free potato stocks from infected wild hosts in "isolated" areas.

Potato leaf roll (PLR), although known since the middle 1700s, was not recognized as a specific disease of potato until 1905 (1); and, until the definite recognition of the transmission of a virus (3,23), was thought to have varied causes. In 1914, Orton (22) wrote, "The literature on leaf roll has become so voluminous that few will undertake to peruse all the contributions, which are, indeed, of very uneven merit, and anyone who attempts it is likely to emerge with his concepts of the disease more confused and hazy than at the start." The confusion associated with this disease has persisted through recent years in regard to its mode of vector transmission (circulative or multiplicative) (14,17,29), type of nucleic acid (26,28), and even etiology (4,30).

Recently, workers have shown that isolates of potato leaf roll virus (PLRV) from Canada, Europe, and Japan contain RNA and are serologically related (26). A California isolate of PLRV, studied earlier, did not react with beet western yellows virus (BWYV) antiserum and did not appear to be closely related to BWYV in cross-protection tests (10).

Recent evidence, however, indicates that although BWYV antiserum does not react with PLRV in common serological tests, antiserum to PLRV reacts with BWYV (J. E. Duffus and R. Stace-Smith, *unpublished*). Antiserum to BWYV did react weakly with PLRV in recent electron microscope serological tests (24). This and other evidence with different luteoviruses now indicates a close affinity of PLRV with the luteoviruses (25).

The recent discovery of an apparently new luteovirus, Solanum yellows virus (20), that affects only solanaceous hosts, supports the possibility that the potato leaf roll disease may be caused by a complex of yellowing agents. Proof of a complex etiology would eliminate some of the confusion that has been associated with this disease since its discovery. Before these studies were published, any persistent aphid-transmitted virus entity isolated from potato was considered to be PLRV. At least, no other criteria were revealed by a pursual of the literature on this disease. Except for serological tests, there is very little evidence of the use of diagnostic techniques, including host range or aphid technology, to differentiate PLR-inducing entities.

This paper describes studies of BWYV isolates obtained from leaf roll-affected potato plants from commercial California and Oregon potato stocks exhibiting typical PLR symptoms.

MATERIALS AND METHODS

Three potato leaf roll-affected potatoes originally were obtained from commercial California potato stocks selected as having PLR symptoms and have been maintained vegetatively in the greenhouse for over 10 yr. Two additional potato leaf roll-affected potatoes were obtained from Oregon. Beet western yellows virus isolates came originally from radish (*Raphanus sativus* L.) ST-1; broccoli (*Brassica oleracea* L. var. *botrytis* L.) ST-7, ST-9, ST-12; malva (*Malva parviflora* L.) ST-11; and lettuce (*Lactuca sativa* L.) ST-E. Turnip yellows virus (TuYV) originally came from turnip (*Brassica rapa* L.) and beet mild yellowing virus (BMYV) came from beet (*Beta vulgaris* L.). The isolates were maintained in desiccated plant tissue.

For activation of virus strains, desiccated tissue was ground in 0.05 M phosphate buffer (pH 7.0) containing 0.01 M glycine (1:1, w/w). Extracts were placed directly on sucrose density-gradients (20–60%) centrifuged 2 hr at 73,450 *g* in a Beckman SW 50.1 rotor, and (after dilution with buffer to 20% sucrose) virus zones (18–26 mm from the top of the tubes) were fed to aphids (7).

The handling of BWYV strains, membrane feeding techniques, and antigen and antiserum preparation for BWYV were as reported previously (7,9,15). Extracts for BWYV antigen preparations, infectivity neutralization, and antigen scanning pattern analyses were prepared from shepherd's purse (*Capsella bursa-pastoris* [L.] Medic.). Frozen plant material was ground in a food grinder 1:1 (w/v) with 0.05 M phosphate buffer, pH 7.0, containing 0.01 M glycine and then homogenized at 45,000 rpm in a VirTis homogenizer. Crude extracts were heated to 45 C, clarified by low-speed centrifugation (20 min, 12,100 *g*), and then pelleted by high-speed centrifugation (2 hr, 80,800 *g*). Pellets were resuspended in 0.05 M phosphate buffer, pH 7.0, containing 0.01 M glycine.

Gradients were made by layering 4, 7, 7, and 7 ml, respectively, of 10, 20, 30, and 40% sucrose dissolved in 0.05 M phosphate buffer, pH 7.0, containing 0.01 M glycine. Centrifugation was done in a Beckman SW-25 rotor for 4 hr at 58,000 *g*. Gradients were scanned photometrically with an ISCO Model D density-gradient fractionator operated on the sensitive scale (A_{254nm}= 0.5).

All density-gradient fractions used in feeding extracts were adjusted to 20% sucrose (by dilution with buffer) before being placed on membranes for acquisition test feeding by aphids.

Aphids that had fed through membranes were tested for virus transmission to shepherd's purse and *Physalis floridana* Rydb. seedlings. Aphids from virus-free colonies, which did not have

access to virus, were tested on these hosts as controls.

Virus assays from the original potato sources and for host range studies were conducted with detached leaves and stems. The samples were washed, surface moisture was removed, and they were placed in petri dishes on moistened filter paper. Approximately 200 nonviruliferous aphids were placed in the dishes with the plant tissue and the dishes were sealed with tape. Aphids were allowed a 24-hr acquisition feeding and were then transferred to test plants for a 48-hr infection feeding interval. They were confined to the test plants by screened sleeve cages.

Nonviruliferous green peach aphids (*Myzus persicae* [Sulzer]) were reared on radish.

Four antisera prepared against different strains of BWYV originally isolated from species of the Cruciferae, Compositae, and Malvaceae, antisera against TuYV (12) and BMYV (13) from Europe, and two antisera prepared against legume yellows virus (LYV) (8) were tested against two isolates of BWYV from potato with leaf roll symptoms and a typical BWYV isolate. Virus-antiserum mixtures were subjected to density-gradient centrifugation, and analyzed photometrically. A positive assay was based on the reduction or elimination of virus antigen in the scanning patterns of density-gradient columns (2,8,11–13).

RESULTS

Virus recovery. The most widely used indicator species utilized in indexing procedures for PLRV has been *P. floridana.* However, a number of viruses (BWYV, BMYV, Physalis mild chlorosis virus, TuYV, PLRV, etc.) cause similar reactions in this host (10). For this reason, in addition to *P. floridana,* shepherd's purse was included as an assay species in attempted recoveries from potato. Shepherd's purse is a commonly used indicator host for BWYV, but is not known to be a host for PLRV.

Even when using relatively large numbers of aphids per test plant (20–30) recovery of any viruses from the PLR-affected potatoes was erratic and transmission efficiency relatively low.

It soon became apparent, however, that in addition to virus isolates inducing symptoms similar to "normal" PLRV (ie, leaf rolling, interveinal chlorosis, petiole epinasty and reduction in leaf size in *P. floridana*) yellowing type pathogens that also infected shepherd's purse occurred in the same plants.

All five potato sources with leaf roll symptoms had naturally occurring isolates that infected shepherd's purse. Primary recovery (ie, recovery directly from potato) was achieved from all five sources. Transmission directly from potato to shepherd's purse was very inefficient; a maximum of 5–10% of the test plants became infected. Initial interveinal yellowing symptoms on shepherd's purse were expressed 5–7 wk after inoculation which is 3–5 wk later than common BWYV strains on that host.

Shepherd's purse-infecting isolates also were recovered from some *P. floridana* plants that became infected during primary recovery tests even though the primary indicator shepherd's purse plants had been negative in the same tests.

In subsequent inoculations of shepherd's purse-infecting isolates to shepherd's purse, *P. floridana*, and potato, differences between the isolates in regard to plant incubation period and symptom severity became apparent. The shepherd's purse-infecting isolates (designated P-1, P-2, P-3, P-4, P-5, P-6, P-7, P-8, and P-9) were distinct from PLRV in host reactions and serological affinities and therefore are considered to be strains or isolates of BWYV. Although repeated serial transfers of *M. persicae* on *P. floridana* test plants have been made, an isolate which does not react with BWYV antiserum and does not infect shepherd's purse has not been recovered from the five potato sources.

Symptoms. The isolates of BWYV from PLR-affected potatoes differ markedly in the severity of symptom expression on *P. floridana* and shepherd's purse. Some isolates induce leaf rolling, interveinal chlorosis, petiole epinasty, and reduction in leaf size in *P. floridana* that is identical to the reported symptoms of PLRV on this host. Others induce various degrees of interveinal yellowing, accompanied by very slight leaf rolling with little stunting or leaf size reduction. Sometimes, 2–3 wk after initial symptom expression, the most mildly affected plants are very difficult to distinguish from healthy plants.

The isolates also differ in response on shepherd's purse as to incubation period and stunting. Although shepherd's purse plants infected directly from potato do not express symptoms for 5–7 wk after inoculation, some isolates have been observed to either change their "affinities" to shepherd's purse or have become masked by more severe strains by serial passage through this host. These isolates show more severe symptoms on shepherd's purse and have incubation periods of 2–3 wk. Other isolates apparently have not changed in their "affinities" to shepherd's purse and have remained mild with long incubation periods. Virus-free Kennebec potatoes and leaf roll-free White Rose potatoes inoculated with two of the BWYV isolates from potato have shown symptoms identical to the original leaf roll plants from which the isolates were obtained and to descriptions of leaf roll symptoms in the literature (ie, an upward rolling of the leaf margins accompanied by interveinal chlorosis and [in some instances] marginal necrosis).

Host range. Host range studies of one isolate (P-5) were carried out by inoculation of 10–20 seedlings of a number of different species with *M. persicae* given 24-hr acquisition feedings on infected shepherd's purse. Presence or absence of virus in each plant species tested for susceptibility was determined by aphid transfer to *C. bursa-pastoris, P. floridana,* and *Nicotiana clevelandii* Gray, 4–6 wk after inoculation.

Host plants of the P-5 isolate of BWYV from potato are: BORANGINACEAE—*Amsinckia douglasiana* DC.; CHENOPODIACEAE—*Spinacia oleracea* L.; COMPOSITAE—*Lactuca sativa* L., *Chrysanthemum coreanum* Hort., *Senecio vulgaris* L.; CRUCIFERAE—*Capsella bursa-pastoris* (L.) Medic., *Lepidium nitidum* Nutt., *Thlaspi arvense* L., *Raphanus sativus* L.; LEGUMINOSAE—*Medicago hispida* Gaertn., *Pisum sativum* L., *Trifolium incarnatum* L., *T. subterraneum* L., *T. vesiculosum* L.; MALVACEAE—*Lavatera trimestris* L., *Malope trifida* Car.; PORTULACEAE—*Claytonia perfoliata* Donn.; SOLANACEAE—*Capsicum annuum* L., *Datura stramonium* L., *Lycopersicon esculentum* Mill., *Nicotiana clevelandii* Gray, *Nierembergia hippomanica, Physalis floridana* Rydb., *P. wrightii* A. Gray, *Schizanthus pinnatus* Ruiz. & Pav., *S. wisetonensis* Hort., *Solanum nigrum* L., *S. polytrichon, S. tuberosum* L., and *Solanum* sp. (PI 174957).

The virus isolate was not recovered from the following species:

TABLE 1. Serological interactions of various luteovirus antisera with isolates of beet western yellows virus from potato

Virus isolate	Reaction of virus after incubation with the indicated serum[a]									
	HSP-5	HSP-7	ST-1-2	ST-9-1	ST-11-1	ST-E-1	TuYV	BMYV	LYV-1	LYV-3
P-5[b]	–	–	+	+	–	+	+	–	+	+
P-7	–	–	+	+	+	+	+	+	+	+
BWYV ST-1	–	–	+	+	+	+	+	+	+	+

[a] Antisera against selected isolates of BWYV (ST-1-2, ST-9-1, ST-11-1, ST-E-1); turnip yellows virus (TuYV); beet mild yellowing virus (BMYV); legume yellows virus (LYV-1, LYV-3); and controls of healthy shepherd's purse (HSP-5, HSP-7).

[b] The virus samples were obtained from infected shepherd's purse, clarified by low-speed centrifugation and pelleted by ultracentrifugation. Pellets were resuspended in buffer to approximately 3.0% of the original volume of sap. The resulting virus samples were mixed with equal volumes of antiserum and incubated 0.5 hr at 37 C. Incubated mixtures were subjected to density-gradient centrifugation (4 hr at 58,000 *g*), and analyzed photometrically. A positive test was based on the reduction or elimination of virus antigen in the scanning patterns of sucrose density-gradient columns.

CHENOPODIACEAE—*Beta vulgaris* L., *Chenopodium capitatum* (L.) Asch., *C. quinoa* L.; CRUCIFERAE—*Brassica oleraceae* L. var. *botrytis* L., *B. oleraceae* L. var. *capitata* L., *B. kaber* (DC.) L. C. Wheeler, *B. marinosa* Bailey, *B. napus* L., *B. pekinensis* (Lour.) Rupr., *B. rapa* L., *Crambe abyssinica* Hochst. ex R. E. Fries; LEGUMINOSAE—*Lens esculenta* Moench; MALVACEAE—*Althaea rosea* (L.) Cav., *Hibiscus diversifolius* L., *H. palustris* L., *H. syriacus, Kitaibelia vitifolia* Willd.; PEDALIACEAE—*Sesamum indicum* L.; PORTULACEAE—*Portulaca oleracea* L.; SOLANACEAE—*Datura tatula* L., *Lycium barbarum* L., *Nicotiana debneyi* Domin., *N. glutinosa* L., *N. tabacum* L., *Physalis heterophylla* Nees, *Solanum melongena* L., *S. stoloniferum* L., a series of *Solanum* sp. plant introductions (PI 116153, PI 174958, PI 196042, PI 200854, PI 202713, and PI 203339), and *Withania somnifera* L.

Serological tests. Antiserum prepared against the strains of BWYV, TuYV, BMYV, and LYV reacted with the isolates from potato and the typical BWYV isolate. However, two antisera (ST-11-1 and TMYV) did not react with the P-5 isolate (Table 1).

Antisera prepared against the P-5 isolate from potato, against typical BWYV (ST-1), and against a Canadian isolate of PLRV supplied by R. Stace-Smith (PLR-Sm), were compared in reactions against five isolates of BWYV, one isolate of TuYV, and the P-5 isolate from potato. All sera reacted with these strains of BWYV. Antiserum against healthy shepherd's purse sap did not react with any of the isolates.

Since the first series of serological tests indicated a differential reaction of two of the BWYV isolates from potato to one antiserum prepared against a BWYV strain and BMYV, further tests were conducted to verify the presence of different BWYV serotypes in potato (Table 2). Four isolates from potato were tested with an antiserum prepared against one of the isolates and another antiserum against a typical BWYV isolate. All of the isolates reacted with BWYV antiserum, but only two of the four isolates reacted with the antiserum prepared against the isolate from potato.

These results and previous work which showed that PLRV did not react with BWYV antiserum in infectivity neutralization (10) and in agar diffusion tests (Duffus and Stace-Smith, *unpublished*) strongly indicate that these virus isolates from leaf roll-affected potato are indeed strains of BWYV. Further, these isolates from potato differ from each other serologically and in reaction to some isolates of BWYV.

DISCUSSION

The recent discovery of an apparently new luteovirus affecting only solanaceous hosts (Solanum yellows virus) (20), but which is closely related serologically to BWYV, indicated the possibility that PLR was caused by a complex of yellowing agents. A complex etiology would help to explain some of the confusion that has been characteristic of this disease since its discovery. For instance, in early work the known hosts of PLRV were restricted to the Solanaceae. Later, Salaman and Wortley (27) reported that PLRV was transmitted to *Campanula, Matthiola,* turnip, and Brussels sprouts. However, Helson and Norris (18) were unsuccessful in transmitting the virus to these species or other crucifers. Natte et al (21) inoculated over 150 species in 39 families and found susceptibility in nine species in the Amaranthaceae and one species in the Nolanaceae. MacKinnon reported the susceptibility of spinach in the Chenopodiaceae (19). Thus, attempts to characterize leaf roll isolates by host range characteristics have resulted in conflicting data. The host range of one BWYV isolate capable of inducing leaf roll in potato and infecting hosts in the Boraginaceae, Chenopodiaceae, Compositae, Cruciferae, Leguminosae, Malvaceae, Portulaceae, and Solanaceae reported herein indicates the importance of reevaluating wild species as PLR reservoirs. It seems probable from the few virus isolates tested here, that wild plant species in a number of plant families may serve as reservoirs of leaf roll-inducing agents in potato-producing and/or seed potato isolation areas.

The isolates of BWYV recovered from leaf roll-affected potatoes reacted serologically the same as other BWYV isolates from beets, crucifers, and composites. All of the isolates reacted with BWYV antiserum, thus distinguishing the entities from a California PLRV isolate tested in the 1960s (10), and the Canadian PLRV isolate of Stace-Smith (Duffus and Stace-Smith, *unpublished*). Antiserum to PLRV reacted with all BWYV strains tested, but the reciprocal reaction (BWYV antiserum against PLRV) has been negative in all tests except the recent distant relationship demonstrated by Roberts et al (24) with an extremely sensitive electron microscope technique.

The host range of the one isolate tested here is similar to other isolates of BWYV, but it seems to have affinities to the Solanaceae and much less affinity to the Brassicas than BWYV strains tested previously.

It is very difficult to separate PLRV isolates from BWYV isolates in the same potato. Both can induce identical symptoms on the *P. floridana* indicator hosts. Serial transfers with continued indexing back to shepherd's purse thus far have failed in our tests. The inability to easily separate PLRV from the complex has serious implications for previous studies on "PLRV" in regard to properties, insect transmission, and serology.

The report of Wright and MacCarthy (31) of the recovery of PLRV from potatoes that did not develop diagnostic symptoms of leaf roll in the field or greenhouse was criticized (4) because these isolates produced only mild symptoms on *P. floridana* and apparently did not cross protect against severe isolates of PLRV. Previous work with BWYV indicates a lack of cross protection between strains of this virus (10). Also, the work reported herein indicates the recovery of several serologically distinguishable and host specific entities from one potato. These results indicate the possibility that Wright and MacCarthy (31) and later Wright and Cole (30) in their reports of mild aphidborne potato virus isolates from various sources in North America were dealing with isolates of BWYV. Certainly their techniques would not distinguish between PLRV and BWYV.

Efforts to rid potato stocks of PLRV by indexing procedures and isolation is a slow and costly process. Recently rapid and economical serological methods (5,6,16) have been suggested as an important alternative. The results of serological studies reported herein, indicate that there are several BWYV serotypes that induce leaf roll. These isolates differ among themselves, from PLRV, and from some isolates of BWYV. The occurrence of these BWYV isolates in potato stocks raises serious questions as to the validity of any currently used serological indexing procedures.

The present studies answer only a few of the important questions concerning the PLR syndrome. However, the results have significant impact on current virus-free potato production and indexing procedures, and on the interpretation of relationship

TABLE 2. Serological interactions of antiserum to an isolate of beet western yellows virus (BWYV) from potato with other isolates from "leaf roll"-affected potato

Virus isolate	Reaction of virus after incubation with the indicated serum[a]		
	HSP-5	ST-1	P-5
P-2[b]	−	+	+
P-3	−	+	−
P-4	−	+	−
P-5	−	+	+
BWYV ST-1	−	+	+

[a] Antisera against healthy shepherd's purse (HSP-5), beet western yellows virus (ST-1), and an isolate of BWYV from potato (P-5).

[b] The virus samples were obtained from infected shepherd's purse, clarified by low-speed centrifugation and pelleted by ultracentrifugation. Pellets were resuspended in buffer to approximately 3.0% of the original volume of sap. The resulting virus samples were mixed with equal volumes of antiserum and incubated 0.5 hr at 37 C. Incubated mixtures were subjected to density-gradient centrifugation (4 hr at 58,000 *g*), and analyzed photometrically. A positive reaction was based on the reduction or elimination of virus antigen in the scanning patterns of sucrose density-gradient columns.

studies.

Studies are continuing on the distribution of BWYV isolates in potato stocks, the economic impact of these isolates, and the occurrence, distribution, and impact of different serotypes on indexing procedures.

LITERATURE CITED

1. Appel, O. 1907. Der Derzeitige stand underer Kentnisse von den Kartoffel krankheiten und ihrer Bekampfung. Mitt. Kaiserl. Biol. Bundesanst. f. Land- Forstwirtsch., Berlin-Dahlem 5:1-31.
2. Ball, E. M., and Brakke, M. K. 1961. Analysis of antigen-antibody reactions of two plant viruses by density-gradient centrifugation and electron microscopy. Virology 39:746-758.
3. Botjes, J. O. 1920. De Bladrolziekte van de Aardappel-plant. 8:1-136. H. Veenen und Zonen, Wageningen, The Netherlands. 136 pp.
4. Bradley, R. H. E. 1978. A search for leaf roll virus that does not cause diagnostic symptoms in potato foliage. Can. Plant Dis. Surv. 58:56-60.
5. Casper, R. 1977. Detection of potato leafroll virus in potato and in *Physalis floridana* by enzyme-linked immunosorbent assay (ELISA). Phytopathol. Z. 90:364-368.
6. Clarke, R. G., Converse, R. H., and Kojima, M. 1980. Enzyme-linked immunosorbent assay to detect potato leafroll virus in potato tubers and viruliferous aphids. Plant Dis. 64:43-45.
7. Duffus, J. E. 1969. Membrane feeding used in determining the properties of beet western yellows virus. Phytopathology 59:1668-1669.
8. Duffus, J. E. 1979. Legume yellows virus, a new persistent aphid-transmitted virus of legumes in California. Phytopathology 69:217-221.
9. Duffus, J. E., and Gold, A. H. 1965. Transmission of beet western yellows virus by aphids feeding through a membrane. Virology 27:388-390.
10. Duffus, J. E., and Gold, A. H. 1969. Membrane feeding and infectivity neutralization used in a serological comparison of potato leaf roll and beet western yellows viruses. Virology 37:150-153.
11. Duffus, J. E., and Milbrath, G. M. 1977. Susceptibility and immunity in soybean to beet western yellows virus. Phytopathology 67:269-272.
12. Duffus, J. E., and Russell, G. E. 1972. Serological relationship between beet western yellows and turnip yellows viruses. Phytopathology 62:1274-1277.
13. Duffus, J. E., and Russell, G. E. 1975. Serological relationship between beet western yellows and beet mild yellowing viruses. Phytopathology 65:811-815.
14. Eskandari, F., Sylvester, E. S., and Richardson, J. 1979. Evidence for lack of propagation of potato leaf roll virus in its aphid vector, *Myzus persicae*. Phytopathology 69:45-47.
15. Gold, A. H., and Duffus, J. E. 1967. Infectivity neutralization - a serological method as applied to persistent viruses of beets. Virology 31:308-313.
16. Gugerli, P. 1978. Potato virus A and potato leafroll virus: Purification, antiserum production and serological detection in potato and test plants by enzyme-linked immunosorbent assay (ELISA). Phytopathol. Z. 92:51-56.
17. Harrison, B. D. 1958. Studies on the behavior of potato leaf roll and other viruses in the body of their aphid vector *Myzus persicae* (Sulz.) Virology 6:265-277.
18. Helson, G. A. H., and Norris, D. O. 1943. Transmission of potato virus diseases. 3. Susceptibility of Cruciferae to potato leaf roll virus. Jour. Counc. Sci. Ind. Res. Aust. 16:261-262.
19. MacKinnon, J. P. 1965. A mild chlorosis virus of *Physalis floridana* found in a turnip latent virus complex. Can. J. Bot. 43:509-517.
20. Milbrath, G. M., and Duffus, J. E. 1978. Solanum yellows, an apparently distinct member of the luteovirus group. Phytopathol. News 12:170.
21. Natti, J. J., Kirkpatrick, H. C., and Ross, A. F. 1953. Host range of potato leafroll virus. Am. Potato J. 30:55-64.
22. Orton, W. A. 1914. Potato wilt, leafroll and related diseases. U. S. Dep. Agric. Bull. 64:1-48.
23. Quanjer, H. M., van der Lek, H. A. A., and Botjes, J. O. 1916. Aard, verspreidingswijze en bestrijding van phloemnecrose en verwante ziekten. Meded. Landbouwhoogesch. Wageningen 10:1-138.
24. Roberts, I. M., Tamada, T., and Harrison, B. D. 1980. Relationship of potato leafroll virus to luteoviruses: Evidence from electron microscope serological tests. J. Gen. Virol. 47:209-213.
25. Rochow, W. F., and Duffus, J. E. 1980. Luteoviruses and yellows diseases. Pages in: Comparative Diagnosis of Viral Disease. Academic Press, New York (In press).
26. Rowhani, A., and Stace-Smith, R. 1979. Purification and characterization of potato leaf roll virus. Virology 98:45-54.
27. Salaman, R. N., and Wortley, W. R. S. 1939. Potential hosts of potato viruses in garden and field. Nature 144:1049-1050.
28. Sarkar, S. 1976. Potato leaf roll virus contains a double-stranded DNA. Virology 70:265-273.
29. Stegwee, D., and Ponsen, M. B. 1958. Multiplication of potato leaf roll virus in the aphid *Myzus persicae* (Sulz.). Entomol. Exp. Appl. 1:291-300.
30. Wright, N. S., and Cole, E. F. 1966. The occurrence of a mild strain of potato leaf roll virus in commercial potato varieties. Am. Potato J. 43:347.
31. Wright, N. S., and MacCarthy, H. R. 1963. Expression and detection of leaf roll virus strains in potato. Am. Potato J. 40:154-162.