Host Range and Properties of a Strain of Tobacco Streak Virus From Potatoes

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ABSTRACT

Salazar, L.F., Abad, J.A., and Hooker, W.J. 1981. Host range and properties of a strain of tobacco streak virus from potatoes. Phytopathology 72:1550-1554.

A virus, coded SB 10, was isolated from potato plants with mild mosaic symptoms. The host range and properties of SB 10 resemble those of tobacco streak virus (TSV). Serological studies and comparative host range with two strains of TSV demonstrated that SB 10 is a new strain. SB 10 is serologically more closely related to TSV-B (originally isolated from soybeans in Brazil) than to the type strain TSV-HF. When inoculated onto potatoes, SB 10 generally causes a mild mosaic or symptomless infection. Progeny tubers from infected mother plants were, except in two clones, virus-free. The virus is probably not a threat to potato production. The virus is readily transmitted through seeds of *Nicandra physalodes* and *Chenopodium quinoa*. Enzyme-linked immunosorbent assay (ELISA) can be used to detect the virus at a concentration of 1 ng/ml or in infected *C. quinoa* sap diluted 10^{-5}.

RESUMEN

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Un virus denominado SB 10, fue aislado de un clon de papa, mostrando un mosaico suave. Su rango de hospederos y sus propiedades son similares a las de tobacco streak virus (TSV). Estudios serlógicos y rango de hospederos en comparación con dos strains de TSV demonstraron que SB 10 es un nuevo strain. SB 10 es más relacionado serológicamente a TSV-B originalmente aislado de soya en Brazil que a TSV-HF el strain tipo. Cuando es inoculado a papa, SB 10 generalmente cuasa un mosaico suave ó infección sin síntomas. Los tubérculos provenientes de plants infectadas fueron hallados libres de virus con excepción de pocos tubérculos en dos clones. SB 10 no parece ser un problema serio en la producción de papa. El virus es transmitido en alta proporción por la semilla de *Nicandra physalodes* y *Chenopodium quinoa*. En pruebas serlógicas de immuno-absorción con conjugado enzimático (ELISA) se pudo detectar al virus en una concentración de 1 ng/ml ó en jugo infectado de *C. quinoa* diluído 10^{-5}.

The high priority placed by the International Potato Center (Centro Internacional de la Papa [CIP]) at Lima, Perú for distributing disease-free potato germ plasm to other countries necessitates the study of previously unknown potato viruses and development of satisfactory diagnostic procedures (6). In recent years, some potentially dangerous viruses thought to be confined to the Andean region have been described (3,10,12–14). The procedure used at CIP to detect virus infections in plant material intended for export combines bioassays, serological tests (enzyme-linked immunosorbent assay [ELISA] and antiserum-sensitized latex [ASL]), electrophoresis, and electron microscopy. By using this testing system, we found a few potato plants infected with a strain of tobacco streak virus, coded SB 10, that in some indicator hosts caused symptoms differing from those induced by previously described potato viruses. This paper describes biological and physical properties of the virus and its serological relationship to tobacco streak virus. A previous report has been published (15).

MATERIALS AND METHODS

Virus isolates and host range tests. The stock culture of SB 10 was obtained from a clone plant of CIP 800174 ([*Solanum phureja* × *S. tuberosum*] × *S. tuberosum*) growing in a screenhouse at La Molina, Lima, Perú. The virus was isolated and maintained by successive transfers to *Chenopodium quinoa*. Inoculations were made by rubbing leaves dusted with Carborundum (600-mesh) followed by a tap water rinse. Back inoculations to *C. quinoa* were made to identify latent infections in hosts.

SB 10 was compared to the type strain of tobacco streak virus (TSV-HF) from tobacco and to TSV-B originally isolated from soybeans in Brazil. Both TSV strains and their antisera were kindly supplied by R. W. Fulton, University of Wisconsin, Madison.

Virus purification. Virus was purified by a modification of the method described by Salazar and Harrison (14) for potato black ringspot virus (PBRV). Infected leaves were homogenized in a blender with 0.06 M sodium phosphate buffer (pH 7.2) containing 0.1% 2-mercaptoethanol (2 ml/g tissue) and 0.001 M ethylenediamine tetraacetic acid (EDTA), and clarified with chloroform (1/5 vol). After centrifugation at 10,000 *g* for 20 min, virus was precipitated from the supernatant fluid with 6% polyethlene glycol 6000 at 4 C for 1 hr. The sediment obtained by centrifuging at 10,000 *g* for 30 min was resuspended in 0.06 M phosphate buffer, pH 7.2, and the virus was further purified and concentrated by two cycles of differential centrifugation and density gradient centrifugation in 10–40% sucrose. Fractions were collected either automatically or manually and virus particles were concentrated by high-speed centrifugation. The yield of SB 10 was 3–6 mg/100 g leaf, assuming $E^{0.1\%}_{260\,nm} = 5.1$.

Electron microscopy. Purified virus was placed onto electron microscope (EM) grids and stained with 1% Na-phosphotungstate (pH 6.5–7.0) or 1% uranyl acetate pH 4.5. Preparations were observed in a JEM-100S electron microscope at 80 kV.

Preparation and electrophoresis of virus protein. Protein samples were prepared by mixing equal volumes of purified virus preparation (1 mg/ml) with sodium dodecyl sulphate (SDS) and 1% 2-mercaptoethanol in 0.01 M sodium phosphate, pH 7.0, and boiling for 3 min (9). Electrophoresis was in gels containing 5–10% acrylamide, 0.12–0.25% methylene bisacrylamide, and 0.1% SDS. Protein bands were detected by staining with Coomassie brilliant blue. SDS-6 marker proteins (Sigma Chemical Co., St. Louis, MO 63178) were used in electrophoresis, and molecular weights were estimated from plots of log molecular weight and migration distances.

Antiserum production and serological studies. An antiserum to SB 10 virus was produced by injecting rabbits intravenously with 1 mg of virus followed by 10 intramuscular injections of 1–2 mg of

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purified virus emulsified with Freund's incomplete adjuvant during a period of 2 mo.

Antibodies were purified and linked to alkaline phosphatase (Sigma) as described by Clark and Adams (1) and used to detect the presence of SB 10 in potato seed clones.

The serological relationship of SB 10 to TSV was studied by titration experiments, cross-reactions, and reciprocal absorption tests in agarose-gel double diffusion tests. Experiments were performed in plates with 0.7% agarose prepared in water containing 0.02% sodium azide.

RESULTS

Isolation, host range, and symptoms of SB 10. An extremely mild mosaic was observed in potato plants of CIP clone 800174 growing in a screenhouse in November 1979 (early summer). Sap from these plants was inoculated onto a selected host range (*Chenopodium amaranticolor* Coste & Reyn., *C. quinoa* Willd, *Gomphrena globosa* L., *Nicotiana clevelandii* Gray, *N. glutinosa* L., and *N. debneyi* Domin.). Tip necrosis and a few local ringspots developed in *G. globosa* and *C. quinoa* and examination of sap from these plants under the electron microscope showed a few isometric particles. This virus infected 20 of 27 species tested in four families. Host range and symptoms were similar to TSV (Fig. 1A), but in these early attempts SB 10 did not infect known hosts of TSV such as *Datura stramonium, D. metel,* or *Lycopersicon esculentum* (4). *C. quinoa* (Fig. 1B) and *G. globosa* were used for diagnostic and infectivity assay purposes. A few hosts reacted with local symptoms, but they were not sufficiently consistent to use in infectivity assays. These included *Cyamopsis tetragonoloba*, which has been previously reported as a local lesion assay host for TSV (4).

TABLE 1. Infection of potato cultivars by sap inoculation with tobacco streak virus strain SB 10

Cultivar	Infection[a]	
	Primary	Secondary
Atzimba	0/2	...
ICA-Puracé	0/3	...
Kennebec	2/2	0/4
Tomasa Condemayta	2/2	1/1
CIP 800174	3/3	2/15[b]
LT-4	2/4	...
María Tropical	0/2	

[a] Primary: numerator = number of infected plants; denominator = number of sap-inoculated plants. Secondary: numerator = number of plants carrying SB 10; denominator = number of tubers planted.

[b] 10/10 tubers from one of these secondarily infected plants carried the virus and showed strong symptoms of leaf deformation.

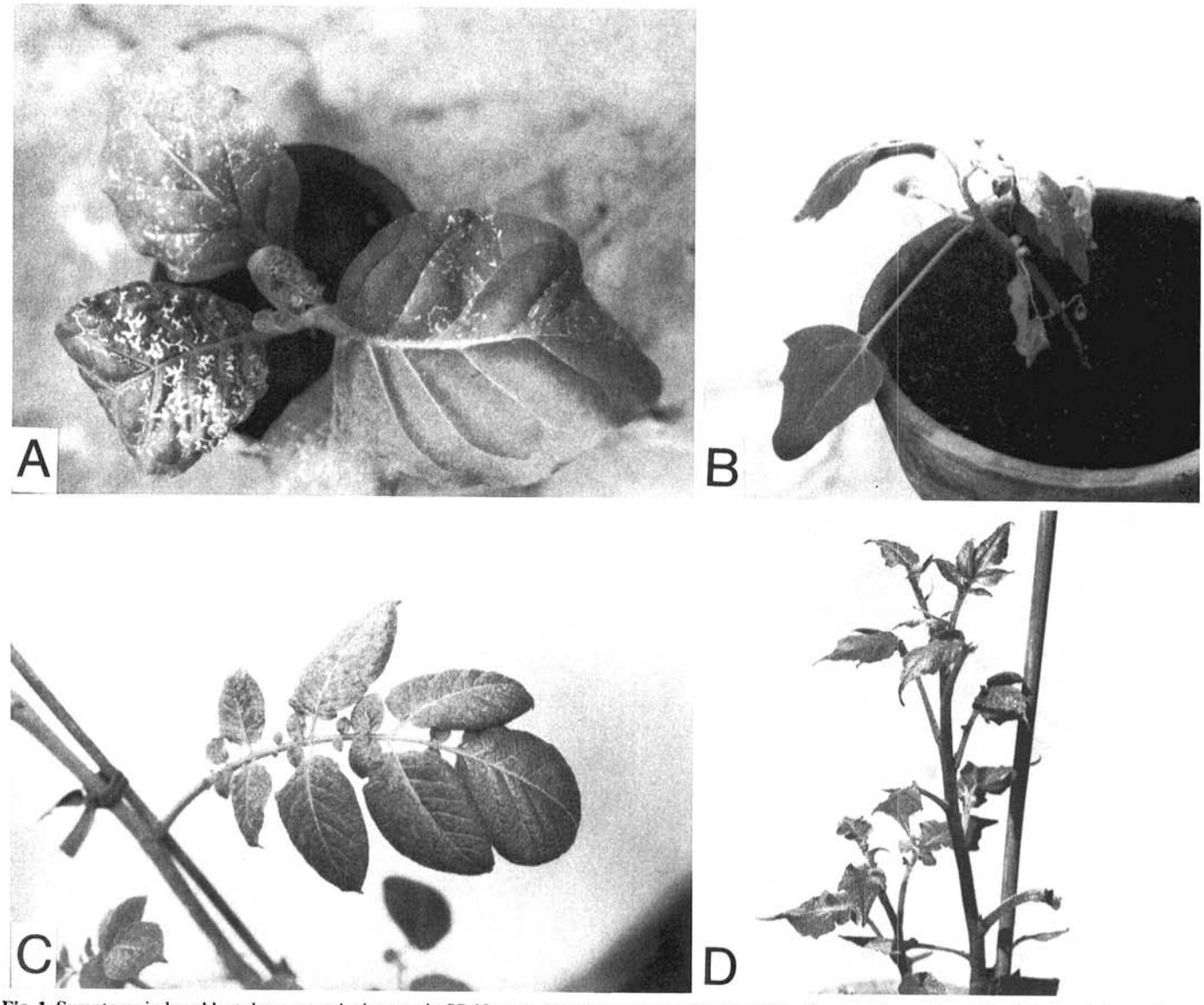

Fig. 1. Symptoms induced by tobacco streak virus strain SB 10 on **A,** *Nicotiana tabacum* 'Samsun'; **B,** *Chenopodium quinoa*; **C,** mild mosaic in a primary infected plant of potato cultivar Kennebec; **D,** secondary symptoms in potato clone DTO-33.

Aphid and seed transmission. Attempts to transmit the virus from infected *C. quinoa* and potato seedlings by *Myzus persicae* Sulz., with acquisition feeding periods ranging from 10 min to 3 days and inoculation periods up to 3 days, were not successful. This property of SB 10 also resembles TSV (9).

Seed transmission was examined in *C. quinoa, Nicandra physalodes,* and *G. globosa.* Seeds from infected plants were collected and germinated in trays containing a mixture of soil and peat. *C. quinoa* seedlings were tested in groups of five whereas those of *N. physalodes* were tested individually. A high percentage of transmission (19 of 20 groups tested) was found in *C. quinoa.* Only eight of 200 seeds of *N. physalodes* germinated. These plants were dwarfed and deformed with narrowed leaf lamina and prominent veins; all contained SB 10. Most plants of *G. globosa* infected with SB 10 did not produce seeds and only one plant produced very few seeds that did not germinate. Seeds from healthy plants of the three hosts had a germination rate above 90% and were free of SB 10.

Infection and symptoms in potatoes. Of seven healthy cultivars of *S. tuberosum* or *S. tuberosum* × *S. andigena* (Table 1) inoculated with SB 10, four became infected and mild mosaic symptoms were observed only in plants of cultivar Kennebec (Fig. 1D). Four tubers from SB 10-infected Kennebec, 15 from CIP 800174, and one from Tomasa Condemayta plants were planted and tested for infection. Infection was detected in a single plant of Tomasa Condemayta and in two plants of CIP 800174, but not in Kennebec. These secondarily infected plants showed severe leaf deformation and vein thickening (Fig. 1C). These results are similar to those of Costa et al (2) and suggest that TSV is rarely prepetuated by tubers. However, 10 tubers from a secondarily infected plant of CIP 800174 produced plants with severe symptoms and all were infected with SB 10.

Properties in sap. SB 10 had a rather low thermal inactivation point (TIP): it was inactivated in *C. quinoa* sap treated at 55 C for 10 min. Its dilution endpoint (DEP) using distilled water as diluent was 10^{-2}. Its in vitro longevity was studied by grinding infected *C. quinoa* leaves in distilled water (1 g of tissue in 4 ml) and storing aliquots of sap at room temperature. SB 10 lost infectivity after storage for 2 hr.

Properties of virus particles. Purified preparations of SB 10 stained with 1 or 2% uranyl acetate (pH 4.5) contained isometric particles about 28 nm in diameter with spherical outlines (Fig. 2). Preparations stained with 1–2% phosphotungstate or ammonium molybdate at pH 6–7 were of low contrast and particles were degraded.

Particles in sucrose density gradients sedimented as three components (Fig. 3). Their sedimentation coefficients estimated by comparison to an unfractionated preparation of PBRV (14) were 85, 98, and 120S. Polyacrylamide gel electrophoresis of proteins from SB 10 preparations detected one major component with a molecular weight ~30,000 daltons. Values obtained in 5 or 10% acrylamide gels did not differ significantly. A second component with a molecular weight ~58,000 daltons in 5% gel and ~54,000 daltons in 10% gel was always obtained. This component is probably a dimer with anomalous migration in gels of high acrylamide concentration.

Testing by ELISA. With 1 mg of purified gamma-globulin and enzyme-linked antibodies at 1/800, as little as 1 ng of virus was detected (Fig. 4). SB 10 was detected in infected *C. quinoa* extracts diluted 10^{-5} (Fig. 4), but not at higher dilution. ELISA was also used to assay SB 10 in seed clones. Sap extracts of 88 clones from the in vitro germ plasm collection at 25 C did not react in ELISA, whereas no infection with SB 10 was found in plants of 30 clones growing in screenhouses during April 1981.

Serological studies. When SB 10 or TSV-B antiserum was cross reacted against homologous antigens and the two strains of TSV, the precipitation line formed to SB 10 and TSV-B produced incomplete fusion of lines and a prominent spur over TSV-HF (Fig. 5). In reciprocal tests with TSV-HF antiserum, homologous reactants spurred over TSV-B and SB 10. Results suggest that SB 10 and TSV-B are more closely related to each other than to the type strain.

Virus antisera were (twofold serial dilutions) tested against purified viruses at a concentration of 40 and 80 μg/ml. With the

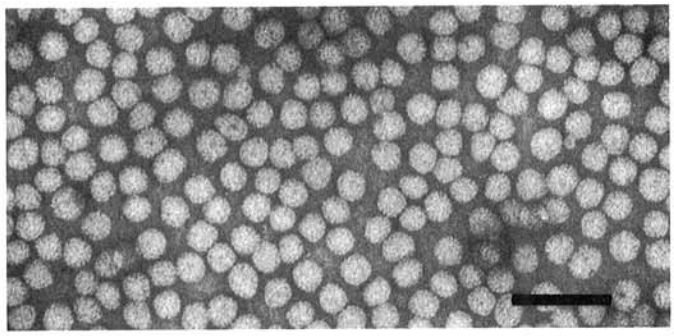

Fig. 2. Electron micrograph of a purified preparation of tobacco streak virus strain SB 10. Particles were stained with 1% uranyl acetate pH 4.5. Bar represents 100 nm.

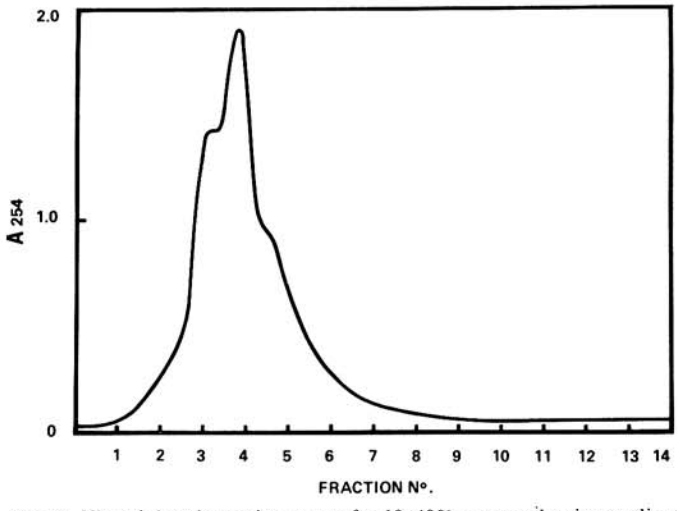

Fig. 3. Ultraviolet absorption scan of a 10–40% sucrose density gradient tube after centrifugation of purified preparation of tobacco streak virus strain SB 10 in a Beckman SW 25.1 rotor at 20,000 rpm for 2 hr. Sedimentation is from left to right.

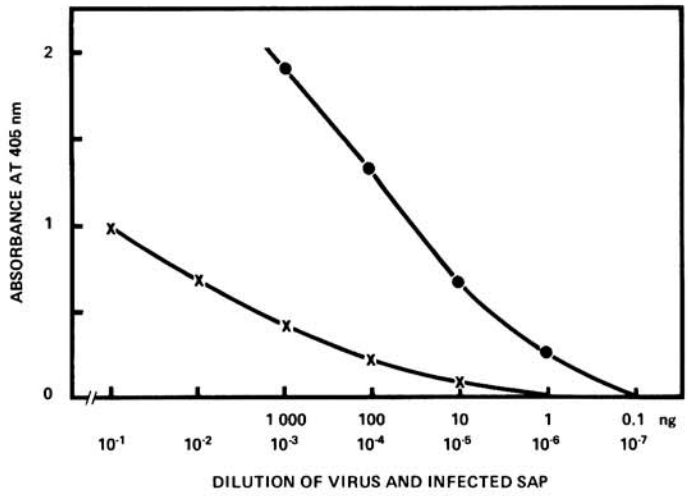

Fig. 4. Enzyme-linked immunosorbent assay (ELISA) values ($A_{405\ nm}$) of dilutions of a purified preparation of tobacco streak virus strain SB 10 (•——•) and dilution of sap extracts of infected *Chenopodium quinoa* plants (×——×). Buffer (PBS) and healthy extract absorbance values were subtracted from those of purified preparation and infective extracts, respectively.

three antisera the heterologous reactions occurred one or two dilutions lower than the homologous reaction (Table 2).

Antisera to the three strains diluted 1/20 with saline were incubated for 2 hr at 37 C in a water bath with their homologous and heterologous viruses at a concentration of 40 and 80 μg/ml. Precipitates were pelleted by centrifugation at 6,000 *g* for 10 min and the supernatant was tested against all virus antigens. To obtain complete antibody absorption, the absorbing virus was loaded in the antiserum wells 16 hr before absorbed antiserum and antigens were loaded in the plates. As expected, when the antisera were absorbed with their homologous virus no reaction occurred (Table 3). On the other hand, absorption of antisera with a heterologous virus removed all antibodies reacting to that virus, but left antibodies that reacted only to the homologous virus and in some combinations to the other heterologous viruses. HF antiserum absorbed with SB 10 did not react with either SB 10 nor TSV-B antigens. A closer affinity between SB 10 and TSV-B can be deduced from patterns obtained after absorbing SB 10 antiserum with TSV-HF since a large proportion of antibodies specific to SB 10 and a few to TSV-B were not absorbed. A similar conclusion can be deduced from patterns of TSV-B antiserum absorbed with TSV-HF virus in which antibodies specific to TSV-B and SB 10 were not absorbed as well as that of TSV-B antiserum absorbed either with SB 10 or TSV-B in which all antibodies were removed. In contrast, the serological distinctiveness between SB 10 and TSV-B is further stressed in the pattern obtained after absorbing SB 10 and antiserum with TSV-B, which demonstrates the presence of some antibodies reacting to SB 10 that are not common to TSV-B. Similarly, the failure of TSV-B to absorb all antibodies reacting with SB 10 from TSV-HF antiserum indicates that TSV-B and SB 10 are serologically distinct strains. Furthermore, this last pattern and the removal with SB 10 of all antibodies from TSV-B antiserum suggest a closer serological affinity between SB 10 and TSV-HF than TSV-HF and TSV-B.

Infection and symptoms caused in selected hosts by TSV and SB 10. To determine if the serological differences between TSV-B, TSV-HF, and SB 10 correlate with differences in infection and symptom production, the three viruses were inoculated onto a selected host range (Table 4). In this test, hosts in the family Chenopodiaceae showed the most striking differences since none of them were infected by TSV-HF and *C. amaranticolor* was not infected by TSV-B. In the Solanaceae, *C. frutescens* and the F_1-hybrid *N. clevelandii* × *N. bigelovii* were not infected with SB 10 whereas both TSV-B and TSV-HF infected and produced symptoms in these hosts. *D. stramonium*, which was not infected with SB 10 in three previous attempts, became infected in this test. To rule out the possibility of contamination of SB 10 with other TSV isolates, comparative host range inoculation was repeated with a sample of the original SB 10 isolate, which had been kept frozen at −20 C. New samples of TSV-B and TSV-HF were also used. Results were similar to previous tests and SB 10 infected four to six inoculated plants of *D. stramonium*. In gel diffusion tests with SB 10 antiserum this original isolate was identical to the isolate of the previous experiment, their precipitation bands spurred over the TSV-HF, but not over TSV-B bands. These results suggest that infection of *D. stramonium* with SB 10 is erratic and may depend on environmental conditions. In general, infection and symptoms with SB 10 and TSV-B were closer to each other than to TSV-HF, which is in agreement with their serological relationship. Differences in the host ranges of SB 10 and TSV-B provide additional evidence that they are distinct strains of TSV.

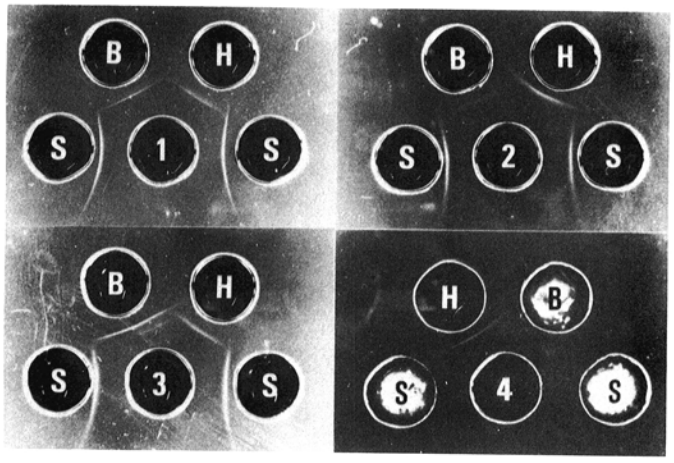

Fig. 5. Gel diffusion reaction and cross-absorption tests between tobacco streak virus strain SB 10 (S), the soybean strain (B), and the type strain (HF) of tobacco streak virus (H). Virus antigens were purified preparations at 40 μg/ml. 1 = Well charged with SB 10 antiserum; 2 = anti-HF serum; 3 = anti-B serum; and 4 = well charged with SB 10 virus and then HF antiserum previously absorbed with SB 10 virus for 2 hr at 37 C.

DISCUSSION

Serological evidence, host range studies, and physical properties confirm that SB 10 is a new strain of TSV. Results of agarose-gel double-diffusion tests and comparative host range suggest that SB 10 is closer to TSV-B found in soybeans in Brazil (R. W. Fulton, *personal communication*) than to TSV-HF the type strain. It is interesting to find this degree of relationship, which provides strong support to the idea that both strains may have evolved from a common TSV ancestor.

Sap and particle properties of the strain herein studied agree with previously reported values for TSV (5). The several differences found in the molecular weight of the coat protein and the observation of probably dimer molecules may only reflect differences in the methods of protein preparation and electrophoresis that were used.

TSV has a wide host range (4) and several strains have been

TABLE 2. Titres[a] of three tobacco streak virus (TSV) antisera in homologous and heterologous combination assayed in agar gel-diffusion tests

Antiserum[b]	Sap from healthy plants	Antigen[c]		
		SB 10	TSV-HF	TSV-B
SB 10	2	64	16	16
HF	2	8	64	16
B	4	16	16	32

[a] Expressed as reciprocals of dilution end point concentration.
[b] Antisera were used in twofold dilutions in saline.
[c] Purified virus preparations were used (40 and 80 μg/ml).

TABLE 3. Reactions in agar gel-double diffusion test of the three TSV antisera absorbed with homologous and heterologous virus antigens

Antiserum[a]	Absorbing virus	Intensity of precipitin line to[b]		
		SB 10	TSV-HF	TSV-B
SB 10	SB 10	−	−	−
	HF	+++	−	+
	B	+	−	−
	none	++	+	++
HF	SB 10	−	+++	−
	HF	−	−	−
	B	+	+++	−
	none	++	+++	++
B	SB 10	−	−	−
	HF	+	−	+
	B	−	−	−
	none	+++	+++	++

[a] Antisera were diluted 1/20, then incubated for 2 hr at 37 C with the absorbing virus at 40 or 80 μg/ml. Results were essentially the same at both virus concentrations.
[b] Symbols: − indicates absence of precipitin line, + indicates a positive reaction, and number of pluses indicates the relative intensity of the precipitin line.

TABLE 4. Comparative infection and symptom types of some host plants with three strains of TSV

Family/Species	Symptoms[a]					
	SB 10		TSV-HF		TSV-B	
	I	S	I	S	I	S
Amaranthaceae						
Amaranthus caudatus	0	0,CS	–	–	–	–
A. edulis	0	M,CRS	–	–	0	M,LD
Gomphrena globosa	NS	NR,LD	NS	NS,LD	NS	NR,LD
Chenopodiaceae						
Chenopodium amaranticolor	0	TN,LD,St	–	–	–	–
C. murale	NS	NS,LD	–	–	NS	NS,LD
C. quinoa	NS	TN,St	–	–	NS	TN,St
Solanaceae						
Capsicum frutescens	–	–	NS	TN,St	NR	Tn,St
Datura stramonium	LD	St	LD	St,LD	LD	St,LD
Nicandra physalodes	0	M,St	NS	M,St	NS	M,St
Nicotiana clevelandii	0	0	0	LD,St,VC	–	–
Nicotiana debneyi	–	M	CS	M,LD	CS	M,LD
Physalis floridana	0	M,LD,St	0	M,LD,St	0	M,LD,St
N. tabacum 'Samsun'	0	VN,M	0	VN,M,LD	0	VN,M
Hybrid F_1 (*N. clevelandii* × *N. bigelovii*	–	–	0	LD,St	0	LD,St

[a] I = inoculated leaves; S = systemically infected leaves; NS = necrotic spots; CS = chlorotic spots; LD = leaf deformation; NR = necrotic ringspot; TN = tip necrosis; St = stunting; M = mosaic or mottle; VC = vein clearing; VN = vein necrosis; 0 = symptomless infection; and – = no infection.

found infecting economic crops (2,5,8,11). The symptoms of TSV in several potato cultivars in Brazil by Costa et al (2) consisting of necrotic spots and rings after mechanical inoculation were never observed with SB 10, which causes a mosaic in infected plants. This difference seems to suggest they are distinct strains of TSV. It will be interesting to examine this further.

Under the conditions of our studies TSV does not seem capable of reducing yield drastically in primary infection and its poor transmission through tubers reduces the possibility of its becoming a severe limiting factor for potato production. However, it becomes important in our efforts to exclude this virus from our genetic materials intended for export. A system of using a combination of methods (6) to detect virus infections guarantees that stocks will be virus-free. Because of its sensitivity, ELISA can be included to detect infections with TSV.

The ability of SB 10, as most other strains of TSV, to be transmitted in high proportion in the botanical seed of some of its hosts justifies efforts to study its behavior in potatoes. It is particularly important to understand its epidemiology since no vector is known for TSV. Furthermore, the study and control of viruses transmitted through botanical seed is important in CIPs attempts to produce potatoes from botanical seed (7). Infection of weeds and other crop species may be suspected of playing important roles for TSV survival and spread as has been suggested for PBRV and potato virus T (13,14).

We propose that SB 10 be called the potato strain of TSV. To our knowledge this is the first report of TSV from naturally infected potatoes in the Andean region of South America.

LITERATURE CITED

1. Clark, M. F., and Adams, A. N. 1977. Characteristics of the microplate method of enzyme-linked immunosorbent assay for the detection of plant viruses. J. Gen. Virol. 34:475-483.
2. Costa, A. S., Carvalho, A. B., and Deslandes, J. 1964. Ocorrencia do virus de necrose branca do fumo em plantacóes de batatinha. Bragantia 23:1-8.
3. Fribourg, C. E., Jones, R. A. C., and Koenig, R. 1977. Andean potato mottle, a new member of the cowpea mosaic virus group. Phytopathology 67:969-973.
4. Fulton, R. W. 1948. Hosts of tobacco streak virus. Phytopathology 38:421-428.
5. Fulton, R. W. 1971. Tobacco streak virus. No. 44 in: Description of plant viruses. Commonw. Mycol. Inst., Assoc. Appl. Biol., Kew, Surrey, England.
6. International Potato Center (Centro Internacional de la Papa). 1977. Annual report. 156 pp.
7. International Potato Center (Centro Internacional de la Papa). 1979. Production of potatoes from true seed. Report of a planning conference. 13–15 September 1979, Manila, The Philippines. 172 pp.
8. Johnson, J. 1935. Tobacco streak, a virus disease. Phytopathology 26:285-292.
9. Mayo, M. A., and Cooper, J. I. 1973. Partial degradation of the protein of tobacco rattle virus during storage. J. Gen. Virol. 18:281-289.
10. Moreyra, A., Jones, R. A. C., and Fribourg, C. E. 1980. Properties of a resistance-breaking strain of potato virus X. Ann. Appl. Biol. 95:93-103.
11. Patiño, G., and Zaumeyer, W. J. 1959. A new strain of tobacco streak virus from peas. Phytopathology 49:43-48.
12. Salazar, L. F., and Harrison, B. D. 1978. Particle properties and strains of Andean potato mottle virus. J. Gen. Virol. 39:171-178.
13. Salazar, L. F., and Harrison, B. D. 1978. Host range, purification and properties of potato virus T. Ann. Appl. Biol. 89:223-235.
14. Salazar, L. F., and Harrison, B. D. 1978. Host range and properties of potato black ringspot virus. Ann. Appl. Biol. 90:375-386.
15. Salazar, L. F., Abad, J. A., and Hooker, W. J. 1981. An ilarvirus affecting potatoes in Perú. (Abstr.) Am. Potato J. (In press).