Natural Hosts and Vectors of Tobacco Streak Virus in Eastern Washington

Walter J. Kaiser, Stephen D. Wyatt, and George R. Pesho

First and third authors, research plant pathologist and research entomologist, respectively, Regional Plant Introduction Station, Washington State University, Pullman 99164; second author, assistant professor, Department of Plant Pathology, Washington State University, Pullman 99164.

We thank Judy Brown, R. O. Hampton, D. Z. Maat, R. Stace-Smith, and R. H. Converse for gifts of antisera to tobacco streak virus; T. Kono for identification of thrips; and A. M. Davis for identification of the plant species. The authors are grateful to G. I. Mink and W. E. Howell for help, advice, and encouragement. We gratefully acknowledge the competent technical assistance of R. M. Hannan and Kathleen Rigert.

Scientific Paper 6179 from the College of Agriculture Research Center, Washington State University, Pullman.

Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture and does not imply approval to the exclusion of other products that may also be suitable.

Accepted for publication 11 June 1982.

ABSTRACT

Kaiser, W. J., Wyatt, S. D., and Pesho, G. R. 1982. Natural hosts and vectors of tobacco streak virus in eastern Washington. Phytopathology 72: 1508-1512.

Tobacco streak virus (TSV) was isolated from naturally infected white sweet clover (Melilotus alba) and cowpea (Vigna unguiculata), but not from other wild plant species at Central Ferry, WA. M. alba, a biennial wild legume, was the primary reservoir and overwintering host of TSV in this region of eastern Washington. The virus was seedborne in 0.7-90.6% of the seed of five artificially infected plant species and in <3% of the seed of naturally infected M. alba plants. Tobacco streak virus was symptomless in naturally or artificially infected M. alba. Five isolates of the virus from cowpea (C1, C2) and white sweet clover (M1, M2, M3) were divided into

two pathotypes, I (isolates C1, C2, M1) and II (isolates M2, M3), on the basis of symptoms produced on several inoculated hosts, particularly *Chenopodium quinoa*, *Phaseolus vulgaris* 'Bountiful,' and *Vicia faba*, and reactions in immunodiffusion tests with TSV antisera from four sources. The two pathotypes appeared to belong to distinct serotypes. Studies of TSV transmission by insect vectors demonstrated that TSV was transmitted from naturally infected *M. alba* to *C. quinoa* and *M. alba* by thrips (*Thrips tabaci* and/or *Frankliniella occidentalis*), but not by pea aphids (*Acyrthosiphon pisum*) or pea leaf weevils (*Sitona lineata*).

Additional key words: virus transmission by thrips.

Many isolates of tobacco streak virus (TSV) differing in host range, symptom expression, physical properties, seed transmission, and serology have been isolated from naturally infected food, forage, and ornamental crops and weed species in North and South America, Europe, and New Zealand (7). In the irrigated region of central Washington, TSV has been isolated from beans (*Phaseolus vulgaris* L.) (17), soybeans (*Glycine max* (L.) Merr.) (21), and asparagus (*Asparagus officinalis* L.) (15,21). There appear to be no reports of TSV infecting these or other crops in the Palouse region of eastern Washington where our studies were conducted.

Tobacco streak virus was one of several sap-transmissible viruses isolated from different crops and weed species growing in or near research plots at Central Ferry, WA. The virus was initially isolated in 1979 from a diseased cowpea (Vigna unguiculata (L.) Walp. 'Clay') plant exhibiting yellow mosaic symptoms. Subsequently, TSV was isolated from naturally infected plants of cultivar California Blackeye cowpea and white sweet clover (Melilotus alba Medik.) at the Central Ferry site.

The Central Ferry station is used by the Regional Plant Introduction Station at Pullman, WA, to increase seed of different plant introductions. Since TSV has a wide host range (6,7) and is seedborne in several wild and cultivated plants (7,11,12), it poses a potential threat to the station's seed production efforts at Central Ferry.

This project was undertaken to assess the importance of alternative hosts, seed transmission, and vectors in the spread and survival of the virus.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. § 1734 solely to indicate this fact.

This article is in the public domain and not copyrightable. It may be freely reprinted with customary crediting of the source. The American Phytopathological Society, 1982.

MATERIALS AND METHODS

Sources of virus. Field studies of TSV were conducted at Central Ferry, and greenhouse and laboratory studies were done at Pullman. The five TSV isolates used were from naturally infected Clay (C1) and California Blackeye (C2) cowpea and M. alba (M1, M2, M3) plants collected at Central Ferry. TSV-C1 was isolated from a cultivar Clay cowpea plant exhibiting yellow mosaic symptoms. The other four TSV isolates were latent in their infected hosts. TSV-M3 was from a M. alba plant infected from seed. Isolates of TSV were selected after serial single-lesion transfer on Cyamopsis tetragonoloba (L.) Taub., and were maintained in Chenopodium quinoa Willd. and M. alba. Inoculum from TSVinfected plants was triturated in 0.01 M phosphate buffer (pH 7.2), 0.06 M K2HPO4, or 0.01 M Na2SO3, to which was added a small amount of 0.22-\mu (600-mesh) Carborundum. Triturate was rubbed on the leaves of young test plants, which were rinsed in tap water immediately after inoculation. Plants included in host-range studies were indexed on healthy C. quinoa at the termination of each experiment after 15-50 days. Inoculated plants were incubated in the greenhouse at 15-25 C.

Seed transmission. Seeds from TSV-C1-infected plants were sown in moist vermiculite, and germinating seeds were transplanted to sterilized soil. Two to four weeks after transplanting, plants were indexed on *C. quinoa* in groups of one to five. If the test plant exhibited symptoms of TSV, each seedling in the pot was indexed individually on *C. quinoa*. Also included in the seed transmission study were seeds from four *M. alba* plants naturally infected with TSV at Central Ferry. Seedlings and test plants were sprayed periodically with pesticides.

Transmission by vectors. At Central Ferry, soil was collected from around *M. alba* plants naturally infected with TSV. Soil was placed in eight 25-cm-diameter plastic pots in the greenhouse. Half of the pots were planted to healthy *C. quinoa*,

cultivar Bragg soybean, and Gomphrena globosa L. seedlings (one plant per pot). The remaining pots were planted to young rooted cuttings of M. alba infected with TSV-C1. After 25 days, healthy C. quinoa and M. alba seedlings were planted in the pots containing TSV-infected M. alba. All bait plants were indexed for TSV on C. quinoa 4-7 wk after planting. Plants were sprayed periodically with malathion to control foliage insects.

Nonviruliferous colonies of pea aphids (Acyrthosiphon pisum (Harris)) from Central Ferry were reared on healthy M. alba in screened cages. Aphids were given acquisition feeding periods of less than 1 min (duration of a single probe) to 10 days on M. alba naturally infected with TSV-M1. Aphids were transferred to healthy C. quinoa and M. alba in groups of 25–100 for a 4- to 6-day inoculation access period. Healthy test plants were also placed in screened cages that contained a TSV-infected plant of M. alba colonized by A. pisum. Aphids were allowed to move freely between the TSV-infected M. alba and test plants for 7–10 days, then the test plants were removed from the cage and sprayed with a pesticide.

Pea leaf weevils (Sitona lineata (L.)) collected from M. alba plants at Central Ferry were caged on healthy and TSV-infected M. alba. After an acquisition feeding period of 7–10 days on M. alba infected with TSV-M1, weevils were transferred in groups of 25–50 to healthy C. quinoa and M. alba plants for inoculation feeds of 4–6 days.

Thrips were collected from M. alba plants at Central Ferry and transferred in groups of 25-50 to screened cages containing different test plants. Cages used in the thrips transmission studies were covered with a fine-mesh nylon screen (110-μm openings) (Tetko, Inc., 420 Sawmill Road, Elmsford, NY 10523), which prevented escape of these tiny insects. Nonviruliferous western flower thrips (Frankliniella occidentalis (Pergande)) and onion thrips (Thrips tabaci Lindeman) collected from healthy bean plants at Pullman were used in the acquisition feeding experiments. Periodically, the bean source plants were indexed on C. quinoa and tested on agar-gel diffusion plates against TSV antiserum. In most transmission tests, a mixed population of these two thrips species in the nymphal and adult stages was used. Thrips were aspirated into clean vials and these were transferred to cages containing test plants. Thrips were given acquisition access feeds of 6-10 days on M. alba infected with TSV-M1. They were then transferred in groups of 10-25 to healthy C. quinoa seedlings for an inoculation feeding period of 4-6 days. All test plants fed upon by the different insect species were indexed on C. quinoa 10-15 days after the termination of test feedings.

Serological tests. Immunodiffusion tests were made in 0.8% Difco agar gels containing 0.85% sodium chloride and 0.02% sodium azide. Healthy and virus-infected plant specimens from Central Ferry were tested against antisera to different spherical

plant viruses. Most of the agar-gel tests made by using TSV antisera were conducted with sap from healthy and virus-infected *C. quinoa* diluted 1:1 with phosphate buffer (pH 7.0) containing 0.85% sodium chloride. The serological relationship among TSV isolates was studied in agar-gel diffusion tests with antisera prepared against TSV isolates from bean (bean red node isolate, R. O. Hampton), cowpea (TSV-C1 from Central Ferry, J. Brown), *Rubus* (R. Stace-Smith), and Brazilian soybean (D. Z. Maat) (8).

RESULTS

Host range and symptoms. Based on host range studies and symptoms, the five TSV isolates were grouped in two pathotypes (Table 1). Isolates of pathotype I (C1, C2, M1) caused systemic necrosis in C. quinoa (Fig. 1A), while isolates of pathotype II (M2, M3) produced chlorotic mottling and malformation in C. quinoa with little systemic necrosis (Fig. 1B). Symptoms of the two pathotypes also differed in Phaseolus vulgaris 'Bountiful,' Vicia faba, and Vigna unguiculata 'California Blackeye' (Table 1). All isolates induced symptomless infection in M. alba.

Field studies. Beginning in May 1981, different annual and perennial plant species growing within 100 m of the Snake River at Central Ferry were indexed on Bountiful bean, California Blackeye cowpea, chickpea (Cicer arietinum L.), and C. quinoa. Most of the annual wild species had started to flower by the time they were indexed for TSV. In addition to host range studies and symptom expression, serological tests were used to identify TSV and other viruses isolated from plants included in the field trials. TSV was isolated from only eight of 33 M. alba plants. The virus was not isolated from (number of plants indexed in parentheses) Achillea millefolium L. (7), Alnus sp. (3), Amaranthus albus L. (23), A. retroflexus L. (23), Amsinckia sp. (2), Artemisia absinthium L. (4), Chenopodium chenopodioides (L.) Aellen (3), C. album L. (21), Cichorium intybus L. (7), Cirsium arvense (L.) Scop. (7), C. vulgare (Savi) Ten. (6), Clematis ligusticifolia Nutt. (3), Dipsacus sylvestris Huds. (5), Erigeron sp. (2), Erodium cicutarium (L.) L'Hér. ex Ait. (5), Euphorbia maculata L. (6), Euphorbia sp. (9), Helianthus sp. (8), Hypericum perforatum L. (5), Kochia scoparia (L.) Schrad. (6), Lactuca serriola L. (4), Lepidium perfoliatum L. (9), Ligustrum vulgare L. (1), Medicago lupulina L. (14), Melilotus officinalis Lam. (6), Mentha arvensis L. (5), Monarda fistulosa L. (6), Nepeta cataria L. (4), Oenothera biennis L. (2), Polygonum sp. (5), Rosa sp. (6), Rumex crispus L. (6), Salix sp. (6), Salsola kali L. (2), Sisymbrium altissimum L. (2), Solanum nigrum L. (10), S. sarrachoides Sendt. (6), Tetradymia sp. (1), Tragopogon pratensis L. (7), and Tribulus terrestris L. (12).

Seeds of California Blackeye cowpea were planted as a trap crop in June 1981 at three sites along the Snake River at Central Ferry. Thirty surviving plants were indexed for TSV 60-65 days after

TABLE 1. Host range and symptoms of five isolates of tobacco streak virus (TSV) comprising two pathotypes from naturally infected cowpea (Vigna unguiculata) and white sweet clover (Melilotus alba) from Central Ferry, WA

	Host reaction of TSV isolates ^a					
	<u></u>	Pathotype I	,	Patho	type II	
	Vig	gna	Melilotus	Meli	lotus	
Test species	CI	C2	MI	M2	М3	
Chenopodium amaranticolor	CLL,LD,Stb	CLL,LD,St	CLL	CLL.LD	CLL,LD	
C. quinoa	NLL,TN,St	NLL,TN,St	NLL,TN,St	NLL,LD,CM	NLL,LD,CM	
Cucumis sativus 'Ohio MR-17'	NS	NS	NS	CM.St	NS	
Cyamopsis tetragonoloba	NLL	NLL	NLL	NLL	NLL	
Gomphrena globosa	RLL,SM,St	RLL,SM,St	RLL,SM,St	RLL,SI	RLL,SI	
Melilotus alba	SI	SI	SI	SI	SI	
Nicotiana tabacum 'Havana 423'	NS	NS	NS	NS	NS	
Phaseolus vulgaris 'Bountiful'	VN,TN,St	VN,TN,RN,St	NLL,TN,St	SM,St	SM,St	
Vicia faba 'Herz Freya'	NS	NS	NS	SN,TN	SN,TN	
Vigna unguiculata 'California Blackeye'	NLL,VN,TN	VN,TN	VN,TN	NS	NS	

^aTest plants were back-inoculated to healthy C. quinoa.

b Symptom abbreviations: CLL = chlorotic local lesions; CM = systemic chlorotic mottle; LD = leaf deformation; SM = systemic mosaic; NLL = necrotic local lesions; NS = not susceptible; RLL = red local lesions; RN = reddening of nodes; SI = symptomless systemic infection; SN = systemic necrosis; St = stunting; TN = tip necrosis; and VN = vein necrosis.

planting. Tobacco streak virus was isolated from four of 30 California Blackeye cowpea trap plants. One of the four TSV-infected cowpeas exhibited yellow mosaic symptoms similar to those induced by alfalfa mosaic virus (AMV). However, the latter virus was not detected in this plant in immunodiffusion tests with AMV antiserum. The other three TSV isolates were symptomless in this host. Two of the cowpea isolates, one of which was designated TSV-C2, produced red node symptoms in Bountiful bean.

Fifteen newly emerged volunteer M. alba plants growing within 5 m of one group of cowpea trap plants also were indexed for TSV in September 1981. Five of the 15 M. alba plants, all symptomless, were infected with TSV. One isolate (TSV-M2) belonged to pathotype II, while the other four produced systemic tip necrosis

TABLE 2. Transmission of cowpea isolate Cl (pathotype I) of tobacco streak virus (TSV) in seed of several sap-inoculated species^a

	Seed tran	smission
Test species	No.	%
Chenopodium quinoa	43/50 ^b	86.0
Glycine max 'Bragg'	58/64	90.6
Gomphrena globosa	2/148	1.4
Nicotiana clevelandii	5/50	10.0
Vigna unguiculata 'California Blackeye'	1/143	0.7

^a Seedlings were sap-indexed on healthy C. quinoa test plants.

TABLE 3. Transmission of two pathotypes of tobacco streak virus (TSV) in seed of four naturally infected *Melilotus alba* plants^a

Plant		Seed transmission ^b		
	Pathotype group	No.	%	
1	I	0/111°	0	
2	I	1/95	1.1	
3	I	1/107	0.9	
4	II	3/142	2.1	

^a Seeds were collected in September 1981 from TSV-infected plants growing at Central Ferry, WA.

symptoms in C. quinoa characteristic of pathotype I isolates.

Seed transmission. Seed transmission of TSV-C1 in five plant species mechanically infected with the virus ranged from 0.7 to 90.6% (Table 2). Over 95% of the Bragg soybean seedlings infected with TSV were stunted and the foliage exhibited mosaic symptoms. Some of the TSV-infected soybean plants produced normal foliage, but the virus could still be isolated from them. However, TSV-infected seedlings of the other plant species tested were symptomless. *Phaseolus vulgaris* was not included in these seed transmission studies because TSV-C1-infected plants failed to produce pods with viable seeds.

Transmission of TSV also was detected in seeds of three of four naturally infected plants of *M. alba* at Central Ferry (Table 3). No symptoms developed in *M. alba* grown from TSV-infected seed. Moreover, growth of infected plants did not appear to be adversely affected when compared to TSV-free plants.

The distribution of TSV-C1 in mature, dry Bragg soybean seeds from TSV-infected plants was determined by assaying dissected seed parts following the procedure of McDonald and Hamilton (13). The seeds were allowed to mature and dry on infected plants and were stored at 4 C for 2-3 mo before use. Seeds were dissected with a sterile scalpel after soaking in sterile deionized water for 17-18 hr. The seed coat, cotyledons, and embryo of each seed were washed separately in running tap water for 30 min. Seed parts were triturated in 1.0 ml of 0.05 M phosphate buffer (pH 7.0) and indexed separately on *C. quinoa*.

Tobacco streak virus was isolated from the seed coats, cotyledons, and embryos of mature Bragg soybean seeds infected with TSV-C1. Seed coats, cotyledons, and embryos of 10 infected seeds were found by separate assays to *C. quinoa* to contain TSV at respective frequencies of 10/10, 9/10, and 10/10. Local lesions induced by these seed-part inocula exceeded 50 lesions per leaf.

Vector transmission. Experiments designed to determine whether or not TSV was soil-transmissible were negative. The virus was never isolated from test plants that were grown in Central Ferry field soil collected from around TSV-infected plants. Moreover, TSV was not detected in test plants that were planted together with TSV-infected plants of *M. alba* in field soil.

When thrips collected from various flowering plants of *M. alba* at Central Ferry were transferred in groups of 25–50 to healthy *C. quinoa*, TSV was transmitted in one of six experiments. However, similar transfers of field-collected pea aphids and pea leaf weevils did not result in transmission of TSV.





Fig. 1. Chenopodium quinoa systemically infected with two pathotypes of tobacco streak virus (TSV) isolated from Melilotus alba from Central Ferry, WA. A, Isolate TSV-M1 (pathotype I) causes necrosis of apical tissues and often premature death of young infected plants. B, Isolate TSV-M3 (pathotype II) causes deformation and chlorotic mottling of the foliage, with little or no necrosis of apical tissues.

^bNumber of TSV-infected plants per number of plants tested.

^b Seedlings were sap-indexed on healthy *Chenopodium quinoa*.

Number of TSV-infected plants per number of plants tested.

When nonviruliferous thrips from healthy beans at Pullman were given acquisition access feeding periods of 6-10 days on TSV-infected M. alba, the virus was transmitted to four of 10 plants of C. quinoa. No transmission of TSV resulted when similar tests were performed with pea aphids and pea leaf weevils. Tests were negative when nonviruliferous thrips were fed for 6-10 days on virus-free M. alba and transferred to healthy test plants of C. quinoa. The thrips assumed to comprise a single species in the acquisition trials were later found to be a mixture of two species, F. occidentalis and T. tabaci.

In July 1981, five M. alba plants infected with TSV-M1 were placed outdoors in a lath house at Pullman. These plants were naturally colonized by T. tabaci. Transfer of thrips in groups of 25-50 at intervals of 14-35 days resulted in transmission of TSV to M. alba (2/8) and C. quinoa (4/8). No TSV infection occurred when thrips (F. occidentalis and T. tabaci) were transferred at periodic intervals from a large TSV-free plant of M. alba located about 50 m from the lath house. Healthy, nonflowering plants of M. alba placed among the five TSV-infected plants of M. alba became infected with TSV within 14 days.

Chenopodium quinoa test plants infected by viruliferous thrips usually exhibited foliar symptoms 6-10 days after the initiation of inoculation access feedings. Infection of this host by TSV was confirmed by gel double-diffusion serology. Since tobacco ringspot virus (TRSV) was reported by Messieha (14) to be transmitted by thrips, plants of C. quinoa infected by viruliferous thrips were tested serologically for TRSV infection, but all tests were negative.

Serological tests. Identity of the five TSV isolates was confirmed by immunodiffusion tests using one or more sources of antiserum prepared against different TSV isolates. None of the TSV isolates reacted with antisera to alfalfa mosaic virus or several isometric viruses, including bean pod mottle, cucumber mosaic, cowpea chlorotic mottle, peanut stunt, southern bean mosaic, tobacco ringspot, and tomato black ring viruses. Precipitin lines of the three isolates in pathotype I fused when tested against TSV antisera (prepared by others) against isolates from bean, cowpea, Rubus, and Brazilian soybean, indicating that the isolates in pathotype I belonged to the same serotype. Pathotype I isolates also were serologically identical to a Washington bean red node isolate of TSV from G. I. Mink. Serological differences existed between isolates in pathotype I and those in pathotype II, which resulted in the development of spurs when tested against TSV antiserum from Brazilian soybean (Fig. 2). Sap from TSV infected C. quinoa was a better antigen source in immunodiffusion tests than sap from naturally infected or artificially inoculated M. alba (Fig. 2).

DISCUSSION

M. alba, a biennial legume, grows profusely along the banks of the Snake River at Central Ferry where it serves as an important host of several viruses, including pea enation mosaic, pea streak, TSV, and one or more potyviruses (W. J. Kaiser, unpublished). Plants of M. alba are also the primary reservoir of TSV in that area. Over 20% of the plants of M. alba indexed shortly after resuming growth in April 1981 were infected with TSV. Symptoms were not apparent in M. alba infected naturally or artificially with 12 TSV isolates from M. alba and cowpea. Although TSV is reported to naturally infect many plant species (1,3,6,7,11), the virus was isolated from only one (M. alba) of the 41 annual and perennial wild plant species indexed at Central Ferry during the spring and summer of 1981. Elsewhere, other plants serve as important reservoirs of TSV, eg, Arctium minus (Hill) Bernh. in Wisconsin (6) and Ambrosia polystachya DC in Brazil (4,11). Some 40 yr ago, M. alba was suspected as harboring TSV and acting as a source of infection for tobacco growing nearby (1,22). Our report, however, appears to be the first demonstrating natural infection of this host under field conditions.

We found TSV to be transmitted in seeds of six plant species, four of which appear to be new records of seedborne hosts of the virus. The virus caused symptomless infections in the new seedborne hosts, Gomphrena globosa, M. alba, Nicotiana clevelandii, and Vigna unguiculata. Seed transmission of TSV in naturally infected hosts has been observed in asparagus (21), bean (20), and soybean (11). We demonstrated that TSV was transmitted in a low percentage (<3%) of seeds of naturally infected M. alba plants at Central Ferry. In nature, seed transmission of TSV in M. alba may be important in dissemination and survival of the virus. Two pathotypes of TSV belonging to distinct serotypes were isolated from plants of M. alba grown from infected seeds.

Since Johnson (10) described TSV 46 years ago, several investigators suspected from the distribution of TSV-infected plants in tobacco and bean fields (1,18,19,22) that a vector(s) was responsible for transmission of the virus from infected cultivated or wild plants located nearby. In 1976, TSV was first reported transmitted by thrips (Frankliniella sp.) from Ambrosia polystachya, an important wild reservoir host of the virus in Brazil, to tobacco and soybean (4). In earlier (3) and subsequent (11) studies in Brazil, unidentified thrips failed to transmit TSV from naturally infected soybeans and weed hosts to indicator hosts, including soybean and tobacco. Our results appear to be the first to establish thrips as vectors of TSV in North America, and additionally identify T. tabaci and or F. occidentalis as vectors of the virus. The thrips used in our acquisition studies were a mixture of F. occidentalis and T. tabaci. The latter species is an efficient vector of another well-known thrips-transmitted virus, tobacco spotted wilt (16). Additional studies will be needed to determine whether F. occidentalis or T. tabaci is the primary vector of TSV at Central Ferry and to clarify other aspects of the virus-vector relationship. Thrips tabaci alone was able to transmit TSV-M1 from naturally colonized M. alba maintained outdoors in a lath house at Pullman.

Spread of TSV in Rubus spp. was found to be flower related and that infected pollen may be a major means of spread of TSV in this crop (2). However, TSV also spread to Rubus plants that were never allowed to flower, suggesting that an aerial vector(s) transmitted TSV to deflowered plants (2). Thrips could have been responsible for spread of TSV to both flowering and deflowered

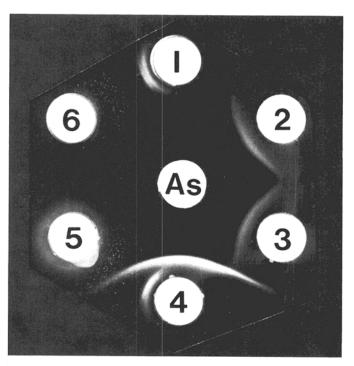


Fig. 2. Agar-gel double-diffusion test between three isolates of tobacco streak virus (TSV) from Central Ferry, WA. The center well (As) contains undiluted antiserum to a Brazilian soybean isolate of TSV. The peripheral wells contain plant sap of: $1 = \text{healthy } Chenopodium \ quinoa; \ 2 \ \text{and} \ 3 = C.$ quinoa infected with two TSV isolates (C2 and M3) (pathotype I) causing necrosis of apical tissues; 4 = C. quinoa infected with a TSV isolate (M2) (pathotype II) causing deformation and chlorotic mottling of the leaves; 5 = M. alba naturally infected with the same TSV isolate (M1) as in well 3; and 6 = healthy M. alba.

Rubus. It seems unlikely that thrips were merely transmitting TSVinfected pollen. In our transmission tests, thrips were transferred from TSV-infected source plants to young test plants of C. quinoa or M. alba that had not flowered.

TSV was isolated from naturally infected soybeans in Iowa (5). The symptoms induced by TSV in soybeans closely resembled those of the bud blight disease of soybean caused by tobacco ringspot virus (TRSV) (5). Subsequently, Ghanekar and Schwenk (9) found TSV to be seedborne in soybean. In 1969, Messieha (14) reported transmission of TRSV by thrips from soybean to soybean. Messieha (14) indicated that the appearance of TRSV symptoms on the foliage of soybean plants infested by thrips differed from those resulting from nematode transmission, suggesting the possibility of infection by another virus. If the virus source plants used by Messieha were doubly infected with TRSV and TSV, which are both seedborne in soybean, thrips may have been transmitting TSV and not TRSV.

Several TSV strains have been isolated from different plant species worldwide (7). These strains differed in host range, symptomatology, physical properties, and/or serology. In Washington, Mink and Uyeda (15) and Uyeda (21) isolated TSV from legumes (bean and soybean) and asparagus, which differed symptomatologically and serologically. In agar-gel diffusion tests, all TSV isolates, except M1, failed to react with antiserum to the asparagus isolates. Legume isolates of TSV from Central Ferry also could be divided into two pathotypes based on symptoms that developed on inoculated test plants, particularly C. quinoa, Bountiful bean, and V. faba, and serology. TSV isolates belonging to pathotype I (C1, C2, and M1) were serologically indistinguishable in immunodiffusion tests using TSV antisera from four sources. Serology and symptomatology showed that pathotype I isolates were very similar, if not identical, to the bean red node strain of TSV. TSV isolates in pathotype II (M2 and M3) were closely related serologically, but distinct from the three TSV isolates in pathotype I as evidenced by formation of spurs in the agar-gel tests. The two pathotypes appeared to correspond to distinct serotypes.

LITERATURE CITED

- 1. Berkeley, G. H., and Phillips, J. H. H. 1943. Tobacco streak. Can. J. Res. 21:181-190.
- 2. Converse, R. H. 1979. Transmission of tobacco streak virus in Rubus. Acta Hortic. 95:53-61.
- 3. Costa, A. S., and Carvahlo, A. M. 1961. Studies on Brazilian tobacco

- streak. Phytopathol. Z. 42:113-138.
- 4. Costa, A. S., and Lima Neto, V. da C. 1976. Transmissão do vírus da necrose branca do fumo por Frankliniella sp. IX Congr. Soc. Bras. Fitopatol. 1 p.
- 5. Fagbenle, H. H., and Ford, R. E. 1970. Tobacco streak virus isolated from soybeans, Glycine max. Phytopathology 60:814-820.
- 6. Fulton, R. W. 1948. Hosts of the tobacco streak virus. Phytopathology 38:421-428.
- 7. Fulton, R. W. 1971. Tobacco streak virus. No. 44 in: Descriptions of Plant Viruses. Commonwealth Mycological Institute, Association of Applied Biologists, Kew, Surrey, England. 4 pp.
- 8. Fulton, R. W. 1972. Inheritance and recombination of strain-specific characters in tobacco streak virus. Virology 50:810-820.
- 9. Ghanekar, A. M., and Schwenk, F. W. 1974. Seed transmission and distribution of tobacco streak virus in six cultivars of soybeans. Phytopathology 64:112-114.
- 10. Johnson, J. 1936. Tobacco streak, a virus disease. Phytopathology 26:285-292.
- 11. Lima Neto, V. da C., Colturato, L. C., Nasser, L. C., Guimarães, O. A., and Thomas, J. C. 1979. Epifitia de queima dos brotos da soja em culturas da região Centro Sul do Paraná. Revista do Setor Ciências Agrárias 1:9-17.
- 12. Mandahar, C. L. 1981. Virus transmission through seed and pollen. Pages 241-292 in: Plant Diseases and Vectors: Ecology and Epidemiology. K. Maramorosch and K. F. Harris, eds. Academic Press, New York. 368 pp.
- 13. McDonald, J. G., and Hamilton, R. I. 1972. Distribution of southern bean mosaic virus in the seed of Phaseolus vulgaris. Phytopathology
- 14. Messieha, M. 1969. Transmission of tobacco ringspot virus by thrips. Phytopathology 59:943-945.
- 15. Mink, G. I., and Uyeda, I. 1977. Three mechanically-transmissible viruses isolated from asparagus in Washington. Plant Dis. Rep. 61:398-401.
- 16. Sakimura, K. 1962. The present status of thrips-borne viruses. Pages 33-40 in: Biological transmission of disease agents. K. Maramorosch, ed. Academic Press, New York. 192 pp.
- 17. Silbernagel, M. J. 1965. 1964 snap bean disease survey in the Pacific Northwest. Plant Dis. Rep. 49:637-638.
- 18. Thomas, H. R., and Zaumeyer, W. J. 1950. Red node, a virus disease of beans. Phytopathology 40:832-846.
- Thomas, W. D., Jr. 1949. Pinto bean diseases in Colorado. Proc. Western Colo. Hortic. Soc. 6:137,139,143,149.
- 20. Thomas, W. D., Jr., and Graham, R. W. 1951. Seed transmission of red node in pinto beans. Phytopathology 41:959-962.
- 21. Uyeda, I. 1978. Identification, characterization, and incidence of viruses isolated from asparagus. Ph.D. thesis. Washington State University, Pullman, WA. 115 pp.
- 22. Valleau, W. D. 1940. Sweetclover, a probable host of tobacco streak virus. Phytopathology 30:438-440.