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Peanut stripe virus – a new seed-borne potyvirus from China infecting groundnut (*Arachis hypogaea*)[1]

BY J. W. DEMSKI, D. V. R. REDDY*, G. SOWELL, JR† AND D. BAYS
Department of Plant Pathology, Georgia Experiment Station, Experiment, Georgia 30212, USA

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A new virus, peanut stripe (PStV), isolated from groundnut (*Arachis hypogaea*) in the USA, induced characteristic striping, discontinuous vein banding along the lateral veins, and oakleaf mosaic in groundnut. The virus was also isolated from germplasm lines introduced from the People's Republic of China. PStV was transmitted by inoculation of sap to nine species of the Chenopodiaceae, Leguminosae, and Solanaceae; *Chenopodium amaranticolor* was a good local lesion host. PStV was also transmitted by *Aphis craccivora* in a non-persistent manner and through seed of groundnut up to 37%. The virus remained infective in buffered plant extracts after diluting to 10^{-3}, storage for 3 days at 20°C, and heating for 10 min at 60°C but not 65°C. Purified virus preparations contained flexuous filamentous particles *c.* 752 nm long, which contained a major polypeptide of 33 500 daltons and one nucleic acid species of $3{\cdot}1 \times 10^6$ daltons. In ELISA, PStV was serologically related to blackeye cowpea mosaic, soybean mosaic, clover yellow vein, and pepper veinal mottle viruses but not to peanut mottle, potato Y, tobacco etch, and peanut green mosaic viruses. On the basis of these properties PStV is identified as a new potyvirus in groundnut.

INTRODUCTION

A disease of groundnut (*Arachis hypogaea*) characterised by dark green stripes and discontinuous banding along the lateral veins of young leaves and oakleaf pattern of older leaves, was first observed during 1982 in Georgia, USA in plants raised from seed imported from the People's Republic of China (Demski, Reddy, & Sowell, 1984). The suspected causal virus was named peanut stripe virus (PStV) on the basis of characteristic stripes observed in young groundnut leaves. In subsequent disease surveys the disease was also observed in the states of Florida, North Carolina, Texas, and Virginia. Symptoms induced by PStV in groundnut differed from those induced by the three previously described viruses of groundnut in the USA, namely peanut mottle (Kuhn, 1965), peanut stunt (Troutman, 1966), and tomato spotted wilt (Halliwell & Philley, 1974) viruses. In this paper we report on the properties of PStV and discuss its importance for future groundnut production in the USA.

MATERIALS AND METHODS

Culture and maintenance. The virus culture was obtained by selecting a symptom-bearing leaf from a groundnut plant, derived from seed imported from China and grown in Spalding

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*Groundnut Improvement Program, ICRISAT, Patancheru, 502324, A. P., India.
†U.S. Department of Agriculture, Regional Plant Introduction Station, Experiment, GA 30212, USA.

Co., Georgia. This leaf was triturated in 0·05 M phosphate buffer, pH 7·2, containing 0·01 M Na_2SO_3 and 1% Celite and the extract rubbed on groundnut seedlings cvs Florunner and Argentine. Subsequent transfer was made to *Chenopodium amaranticolor* which developed local lesions. A single lesion isolate was obtained by four successive single lesion transfers in *C. amaranticolor* and maintained thereafter in *Lupinus albus*.

Host range. At least six plants of each test species were inoculated and 21 days later return inoculations were made from inoculated and uninoculated leaves of test plants to groundnut and *C. amaranticolor*.

Properties in sap. The physical properties of the virus were studied in crude sap of both groundnut and white lupine diluted to 10^{-1} in 0·025 M phosphate buffer, pH 7·2. To determine the thermal inactivation point, 1 ml of sap was heated in a water bath for 10 min.

Seed transmission. Seed from infected groundnut plants that had been grown in a glasshouse was sown in trays of steam sterilised soil and seedlings at the 5th true leaf stage were tested individually for PStV by direct enzyme-linked immunosorbent assay (ELISA).

Effect on yield. Twenty plants each of Florunner and Argentine groundnut, grown in 25 × 20 cm pots, were inoculated when they were 3 wk old with either PStV or with buffer. Following harvest, weights of seed, dried for 3 wk at room temperature (25–30°C), were used to compute yield loss estimates.

Aphid transmission. Aphis craccivora colonies were maintained on cowpea (*Vigna unguiculata* subsp. *unguiculata* cv. California Blackeye). The aphids were starved for 1–12 h and then allowed to make a single acquisition probe of 1 min on detached young infected groundnut leaves. At least 10 insects were then transferred to each healthy Argentine groundnut test plant and after 1 h inoculation access period, aphids were killed by spraying with malathion. All exposed plants were assayed for PStV by inoculation of sap to *C. amaranticolor* and by ELISA.

Virus purification. Infected lupine (*Lupinus albus*) leaves were homogenised in 0·1 M Tris-HCl buffer, pH 8·0, containing 0·02 M Na_2SO_3 and 0·05 M disodium ethylenediaminetetraacetic acid (EDTA) (1 g leaf:4 ml buffer), filtered through cheese cloth and 10% chloroform (v/v) was added and stirred for 3–5 min. The emulsion was broken by centrifuging at 5000 *g* for 10 min. Virus was precipitated by adding 0·2 M NaCl and 4% (w/v) polyethylene glycol (PEG, mol. wt 6000). The precipitate was collected by centrifuging at 10 000 *g* for 10 min, resuspended for 1 h in 0·05 M borate-phosphate buffer, pH 8·3, containing 0·2 M urea (BPU) and clarified at 5000 *g* for 10 min. Twenty ml of the suspension was layered on each 10 ml column of 30% sucrose prepared in BPU containing 4% PEG and 0·2 M NaCl. After centrifuging at 22 500 rev./min for 2 h in a Beckman SW 25·1 rotor, pellets were resuspended overnight in BPU and clarified at 5000 *g* for 10 min. Five ml of the suspension were layered on each of six columns containing 4, 5, 6, and 9 ml of 100, 200, 300, and 400 g/litre of sucrose in BPU and centrifuged at 22 500 rev./min for 2 h in a SW 25·1 rotor. The virus zone was located at 22–25 mm from the meniscus.

Molecular weight determination. The mol. wt of the virus polypeptide was determined in 7·5% and 10% acrylamide gels using a 3·3% spacer gel (Reddy & Black, 1977). Purified virus pellets were resuspended in 0·06 M Tris-HCl buffer, pH 6·8, containing 2% SDS, 1% 2-mercaptoethanol and 6 M urea and co-electrophoresed with markers at 50V for 3·5 to 6 h. The following protein markers (with mol. wts in parentheses) obtained from Bio-Rad were used: Phosphorylase B (90 000), bovine serum albumin (67 000), ovalbumin (43 000), carbonic anhydrase (31 000), soybean trypsin inhibitor (21 000), and lysozyme (14 300).

Nucleic acid was extracted from purified virus by the method of Kirby (1965). Gel electrophoresis was in tube gels (0·6 × 9 cm) containing 2·0% acrylamide and 0·5% agarose. Electrophoresis buffer contained 0·036 M Tris, 0·03 M sodium phosphate, and 0·001 M EDTA, pH 7·8 (Loening, 1969). The PStV nucleic acid samples and marker samples were co-electrophoresed at 50V for 3·5 h. The gels were stained in 0·05% toluidine blue O. Tobacco

mosaic virus RNA (mol. wt $2{\cdot}2 \times 10^6$), and *Escherichia coli* ribosomal RNA's (mol. wts $1{\cdot}05$ and $0{\cdot}55 \times 10^6$ daltons) were used as mol. wt markers.

Antiserum production. One ml of 1 mg virus was emulsified with an equal volume of Freunds' incomplete adjuvant and injected intramuscularly at weekly intervals into two rabbits. Serum was collected 3 wk after the fourth and last injection and titred by the precipitin ring test using purified virus.

Enzyme-linked immunosorbent assay. The direct ELISA (dir-ELISA) procedure used was similar to that described by Lister (1978) and Rajeshwari, Iizuka, Nolt & Reddy (1983) with the exception that antigen buffer contained 0·3 M urea and 0·2% 2-mercaptoethanol. PStV and peanut mottle virus γ-globulins were used at 10 μg/ml and all other antisera were used at 50 μg/ml. The enzyme conjugates were used at 1/500 or 1/250 dilution.

For indirect ELISA the γ-globulins were precipitated with 18% (w/v) sodium sulphate, diluted to 2 mg/ml, treated with 100 μg of pepsin as described by Barbara & Clark (1982), and subsequently dialysed for 2 days in a buffer containing 0·005 M Na_2HPO_4, 0·001 M KH_2PO_4, 0·8% (w/v) NaCl and 0·02% sodium azide, at pH 7·4. Wells of microtitre plates were coated for 2·5 h at 37°C with 0·5 μg/ml $F(ab')_2$ fragments and antigen extracts were incubated overnight at 4°C. PStV and heterologous antisera were added at 1/50 000 dilution (0·25 μg/ml) and incubated for 2·5 h at 37°C. Fc portion of antirabbit γ-globulins prepared in goats (Cappel Laboratories) were conjugated with alkaline phosphatase as described by Clark & Adams (1977) and used at a dilution of 1/1500.

All ELISA reactions were assayed by reading absorbance at 405 nm in a Dynatech ELISA reader. All tests were done in triplicate using at least five replications for each test.

Electronmicroscopy. Measurements were made on particles in crude sap from infected lupine leaves. Staining was with 2% ammonium molybdate, pH 6·5. The grids were viewed in a Philips 201C electron microscope at an instrument magnification of × 13 500. Particle numbers in viewing fields, chosen randomly from different grid squares, were counted on two duplicate grids. Results represent mean values from two grids. The microscope was calibrated using a carbon grating replica with 2160 lines per mm.

Infected groundnut and lupine leaves were processed for thin sections as described by Reddy *et al.* (1983).

Host range and symptomatology. Groundnut plants mechanically inoculated with PStV showed discontinuous stripes along the lateral veins on young quadrifoliates 12–14 days after inoculation (Plate, fig. 1). Later, the older leaves developed a mosaic in the form of green islands (Plate, fig. 2) or oakleaf patterns (Plate, fig. 3). Infected plants were stunted and unlike peanut mottle (Kuhn, 1965) and peanut green mosaic (PGMV) (Sreenivasulu *et al.*, 1981) symptoms persisted in older leaves.

Numerous chlorotic local lesions were produced on *C. amaranticolor* (Plate, fig. 4) and *C. quinoa* leaves 8–10 days after inoculation without systemic infection.

Systemic mosaic symptoms were observed on, and PStV recovered from, leaves of *Glycine max* (cv. Yelredo), *Lupinus albus*, *Nicotiana benthamiana*, *Trifolium incarnatum*, *T. subterraneum*, *T. vesiculosum*, and *Vigna unguiculata* subsp. *unguiculata* (cv. California Blackeye).

The virus did not induce symptoms nor could the virus be recovered from inoculated or uninoculated leaves of *Citrullus lanatus* (cv. Charleston Grey), *Cucurbita pepo* (cv. Early Yellow Summer Crookneck), *Cucumis sativus* (cv. Burpee Pickler), *N. glutinosa*, *N. tabacum* (cv. Burley 21), *Phaseolus vulgaris* (cv. Topcrop), *T. pratense* (cv. Kenland), and *T. repens* (cv. Tillman).

Physical properties. The thermal inactivation point of the virus was between 60°C and

65°C, and the dilution end point between 10^{-3} and 10^{-4}. The virus remained infective in crude sap for 3 days at 20°C.

Seed transmission. Seed transmission ranging from 19·3 to 37·6% (Table 1) occurred in seedlings derived from groundnut seed, collected from plants infected with PStV when young. In addition seed lots of PI 461428, 407462 and 461434 imported directly from the People's Republic of China contained PStV to the extent of 0·4, 0·4 and 2·8%, respectively. It is presumed that these seed lots were derived from a mixture of PStV infected and healthy plants.

Table 1. *Seed transmission of peanut stripe virus in three groundnut genotypes*

Genotype†	Number of seeds tested	Number of infected seedlings	Percent seed transmission**
Argentine	418	157	37·6
PI 461434*	312	94	30·1
Florunner	192	37	19·3

†Healthy plants were mechanically inoculated and maintained in a glass house until harvest.
*Introduced from the People's Republic of China.
**All seedlings were tested individually by ELISA.

Table 2. *Absorbance values (A_{405}) in direct ELISA of homologous and heterologous reactions using peanut stripe virus and 10 other potyviruses*†

	Dilutions of groundnut leaf extracts that were:*					Dilution of homologous antigens from host sap*		
	Healthy		Peanut stripe-infected					
Antiserum to:	10^{-2}	10^{-3}	10^{-2}	10^{-3}	10^{-4}	10^{-2}	10^{-3}	10^{-4}
Bean yellow mosaic virus	0·00	0·00	0·00	0·00	0·00	NA		
Blackeye cowpea mosaic virus from Georgia	0·25	0·03	1·54	0·24	0·00	2·20	1·91	0·95
Blackeye cowpea mosaic virus from Florida	0·12	0·05	1·30	0·32	0·01	2·2	1·78	0·69
Clover yellow vein virus	0·00	0·00	1·08	0·07	0·00	NA		
Peanut green mosaic virus	0·00	0·00	0·00	0·00	0·00	NA		
Peanut mottle virus	0·00	0·00	0·00	0·00	0·00	2·20	2·20	0·96
Peanut stripe virus	0·19	0·00	2·20	1·14	0·38			
Pepper veinal mottle virus	0·00	0·00	0·13	0·00	0·00	NA		
Potato virus Y	0·00	0·00	0·00	0·00	0·00	2·15	1·49	0·92
Soybean mosaic virus	0·24	0·09	0·80	0·30	0·04	2·18	1·64	0·65
Tobacco etch virus	0·00	0·00	0·00	0·00	0·00	1·50	0·76	0·09

†Details described in the text.
*Dilutions are based on the original weight of tissue.
NA = Not available for testing.

Effect on yield. In Argentine and Florunner groundnut, PStV caused 23% and 21% loss in yield, respectively.

Aphid transmission. After a 1 min acquisition access period, *A. craccivora* transmitted the virus to 11 of 14 groundnut plants. None of the five plants exposed to aphids from colonies on healthy plants were infected.

Purification. Under glasshouse conditions, maximum infectivity from systemically infected lupines was obtained 3 wk after inoculation. Several purification procedures were attempted

initially including those used for peanut eyespot virus (Dubern & Dollet, 1980), peanut mottle virus (Rajeshwari *et al.*, 1983, Tolin & Ford, 1983) and clover yellow vein virus (McLaughlin, Barnett, Burrows & Baum, 1981). The procedure used was a modification (extraction buffer changed to 0·1 M Tris, 0·02 M Na_2SO_3, and 0·05 M EDTA adjusted to pH 8·0) of the method developed for PMV (Rajeshwari *et al.*, 1983) and consistently yielded 50–70 mg (assuming an extinction coefficient of 3·0) virus from 1 kg tissue. Purified virus retained 25% of the infectivity present in crude extracts prior to chloroform treatment. Electron microscopy of purified preparations stained with 1% uranyl acetate revealed no observable host contamination. The u.v. absorption spectrum of the purified virus had a shoulder at 290 nm and the $A_{260/280}$ was 1·23. The $A_{260/245}$ was 1·26.

Molecular weight of PStV polypeptide and nucleic acid. In both 7·5% and 10% acrylamide gels, PStV protein preparations contained a major polypeptide of 33 500 daltons and a minor polypeptide of 29 000 daltons (Plate, fig. 6). The PStV nucleic acid assumed to be RNA, migrated as a single band with an estimated mol. wt of $3·1 \times 10^6$ daltons.

Serological relationships. In dir-ELISA, PStV cross reacted strongly with blackeye cowpea mosaic virus (BICMV), clover yellow vein virus (CYVV), and soybean mosaic virus (SMV) antisera. With the exception of a weak reaction with pepper veinal mottle virus (PVMV) antiserum, none of the other potyvirus antisera tested reacted with PStV (Table 2). In indirect ELISA, using $F(ab')_2$ fragments, PStV reacted strongly with antiserum to BICMV, CYVV, and to a lesser extent with PVMV and SMV (Table 3).

Table 3. *Absorbance values (A_{405}) obtained in indirect-ELISA using peanut stripe virus and antiserum to 10 other potyviruses*†

Antiserum to:	Dilutions of peanut stripe-infected groundnut extracts* 10^{-2}	10^{-3}	10^{-4}
Bean yellow mosaic virus	0·00	0·00	0·00
Blackeye cowpea mosaic virus from Georgia	1·02	0·48	0·00
Blackeye cowpea mosaic virus from Florida	0·89	0·42	0·00
Clover yellow vein virus	0·91	0·43	0·00
Peanut green mosaic virus	0·00	0·00	0·00
Peanut mottle virus	0·00	0·00	0·00
Peanut stripe virus	2·20	0·91	0·27
Pepper veinal mottle virus	0·21	0·07	0·00
Potato virus Y	0·00	0·00	0·00
Soybean mosaic virus	0·65	0·15	0·00
Tobacco etch virus	0·00	0·00	0·00

†Details described in the text.
*Dilutions are based on original weight of tissue.

Electronmicroscopy. In thin sections of infected groundnut tissue, cylindrical cytoplasmic inclusions were observed (Plate, fig. 5). Virus particles in purified preparations stained with 2% ammonium molybdate, pH 6·5, had a mean diameter of 13 ± 1 nm and a mean length of 752 nm (mean of 330 particles).

DISCUSSION

PStV is identified as a potyvirus based on serology, size and morphology of its particles, the presence of cylindrical inclusion bodies in infected plants, aphid transmission, and mol. wt of its coat protein subunit and nucleic acid. It has been introduced into the USA through

seed imported from the People's Republic of China. PMV, a potyvirus occurring naturally in groundnut (Kuhn, 1965; Herold & Munz, 1969; Rajeshwari *et al.*, 1983), is distinct from PStV serologically, and in host range and in symptomatology in groundnut. Additionally, in groundnut seed transmission of PMV is 2% or less, whereas that of PStV is much higher. Peanut green mosaic virus, another potyvirus which occurs naturally in groundnut (Sreenivasulu *et al.*, 1981), also differs from PStV serologically, by inducing local lesions on *Phaseolus vulgaris* and it is not seed transmitted in groundnut. PStV also differs from another naturally occurring potyvirus in groundnut, peanut eyespot virus (PESV), in host range and in symptoms in groundnut and, whereas PESV is serologically distinct from CYVV (Dubern & Dollet, 1980), PStV is serologically related to CYVV.

PStV also differs from the other potyviruses to which it is serologically related. Thus, groundnuts inoculated with BICMV, CYVV, and SMV did not show symptoms, and the viruses could not be detected by mechanical transmission or by ELISA. In intragel cross-absorption double diffusion tests (Lima, Purcifull & Hiebert, 1969), PStV is clearly distinct from CYVV and SMV by forming additional precipitin bands. PStV appears most closely related to BICMV using double diffusion gel serology, but differs in other aspects. Thus, (a) BICMV induces tight tube inclusions in cowpea whereas PStV induces tubes plus laminated aggregates, (b) BICMV is seed transmitted in cowpeas, but PStV is not, (c) in both direct and indirect ELISA the homologous titre of PStV antiserum was higher than that against BICMV.

Xu, Yu, Liu & Barnett (1983) reported a seed-borne potyvirus inducing peanut mild mottle disease (PMMV) from the People's Republic of China. In their tests, the virus did not react with CYVV and SMV antisera but reacted weakly with PMV antisera. In our tests, PMMV (obtained from Dr O. W. Barnett) reacted strongly with PStV antiserum in several dir-ELISA tests, giving similar absorbance readings to that obtained with PStV. Furthermore, it induced similar symptoms to PStV in *C. amaranticolor* and *L. albus*. Although some differences were found between PStV and PMMV, we believe they are strains of one virus for the following reasons: they are closely related serologically, they infect and are seed transmitted in groundnuts, symptoms in infected groundnuts are similar (although those induced by PMMV are milder) and they each originated from the People's Republic of China.

Yield loss estimates for PStV and PMV infected groundnuts were made under similar glasshouse conditions and both viruses induced approximately a 20% loss. Field experiments with PStV are not being done because of its potential dissemination. However, PStV causes similar yield losses to PMV (Kuhn & Demski, 1975), but has the potential to spread more rapidly because of its higher frequency of seed transmission. Therefore, assuming the 1984 US groundnut production is 1·7 million tons, a 50% incidence of PStV could incur losses amounting to 85 million US dollars.

Twelve commonly grown groundnut cultivars in the USA and 20 plant introductions were all susceptible to mechanical inoculation with PStV and Xu *et al.* (1983) reported no resistance to PMMV in 663 groundnut germplasm lines tested. Further screening of groundnut germplasm for PStV resistance and for non-seed transmission of PStV are in progress.

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EXPLANATION OF PLATE

Figs 1–3. Leaves of groundnut cv. Argentine infected with peanut stripe virus (PStV) showing:

Fig. 1. Stripe symptom.

Fig. 2. Mosaic symptom.

Fig. 3. Oakleaf mosaic symptom.

Fig. 4. Local lesions induced by PStV in a leaf of *Chenopodium amaranticolor*.

Fig. 5. Electron micrograph of a thin section of PStV-infected groundnut showing cylindrical inclusions. Bar represents 1100 nm.

Fig. 6. Electrophoresis of coat protein subunit of PStV in 10% acrylamide gels. (Details in text). Left: marker proteins. Middle: PStV polypeptides. Right: PStV polypeptides co-electrophoresed with markers.