



Peanut Stripe Virus

CCG GAG GCG GCG GGA GGA GGA GAG ATT GAG AAT GAG
 G C N A G G N N K I G G G G G G G G G G G
 GGA AGA AAG AGA ATG AAT TGG CCA ATG
 R T L K R M G P M G R G N V
 GCG TTG AAT TTA GAT CAA CTT TGG GAT TAC AAG TCA GAG GAA AAT
 G G L L D L L R Y F Y E Q I
 G G T I AA ACA ACA GCG ACG AAG ATG CAG TTT CAA ATG TCG
 D L F N I R A I K M G Y E M W
 AG AAT GC GH AAG GGC GAG TAI GAA ATA TAT GCG GAA GAG AAT
 Y H G G G E Y E I D E I G M
 GGA TTT CTT G G AAT GGC T G ATC GTC TGG TGT TTT TAC AAT GCG
 T I V G N G F M V W G I D N G
 GT GGA GCG GAT GTA T GGA ACA GAG GCG ATC ATG GAC GCA GAC
 F S P D G N G G W V M M D G D
 GGA GAA GTG GAA TAT CCG CCG AAA CCA GAT GTT GAG GAT GCA AAA
 F Q V E Y P K P D V E D A E
 GGA GGA GTT G G CAA ATG AAT TTT GAT TTT TCA GAT GCA GAT GAT
 G G L R Q I T D G G G S L A G I
 GGA TAG GGA ATG AGA AAT TCG GCG TTA CCA G G G G G G G G G G
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Peanut Collaborative Research Support Program

International Crops Research Institute for the Semi-Arid Tropics

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Abstract

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Peanut stripe virus (PStV) is a member of the potyvirus group; it is transmitted mechanically, by aphids (nonpersistently) and through groundnut (*Arachis hypogaea*) seed. PStV naturally infects groundnut in India, Indonesia, Malaysia, Myanmar, People's Republic of China, Philippines, Thailand, USA, and Vietnam. Different isolates of PStV induce different symptoms in groundnut. In the USA, a striping symptom is common; however, in Southeast Asia the most common symptoms are dark green blotches and ring spots. One good local lesion host is *Chenopodium amaranticolor* and the propagation hosts are *Lupinus albus* and *Nicotiana benthamiana*. Antisera have been produced for several PStV isolates and serological tests to detect the virus in foliage and seed are available. Based on serology and peptide profiling of the coat protein, PStV is related to blackeye cowpea mosaic virus. Studies on the genome organization of PStV at the molecular level have been initiated, and the information available so far suggests that it is closely related to soybean mosaic virus, watermelon mosaic virus, and zucchini yellow mosaic virus with an amino acid sequence homology of about 74%. Resistance to PStV has not been identified in commercial cultivars of groundnut. Based on available epidemiological information, disease management strategies are discussed.

Résumé

Virus de la striure de l'arachide. Le virus de la striure de l'arachide (peanut stripe virus ou PStV) appartient au groupe des potyvirus. Il se transmet mécaniquement, par les pucerons (de manière non persistante) et par les graines de l'arachide (*Arachis hypogaea*). Le PStV infecte l'arachide naturellement en Chine, en Inde, en Indonésie, en Malaisie, au Myanmar, aux Philippines, en Thaïlande, aux Etats-Unis et au Viet-Nam. Les symptômes induits chez l'arachide varient selon les isolats différents du PStV. Aux Etats-Unis, le symptôme de striure est courant. Cependant, en Asie du Sud-Est, les symptômes les plus communs sont les taches foliaires (blotches) vert foncé et les taches annulaires. *Chenopodium amaranticolor* est un bon hôte des lésions locales, alors que *Lupinus albus* et *Nicotiana benthamiana* sont des hôtes de propagation. Des antisérums ont été produits pour plusieurs isolats du PStV et des tests sérologiques sont disponibles pour la détection du virus au niveau des feuilles et des graines. D'après la sérologie et la détermination du profil des peptides du protéine de revêtement, le PStV est apparenté à la mosaïque du niébé (blackeye cowpea mosaic virus). Des études sur l'organisation génomique du PStV au niveau moléculaire ont été initiées. Les données disponibles jusqu'à maintenant laissent croire que ce virus est étroitement lié au virus de la mosaïque du soja, à la mosaïque de la pastèque (watermelon mosaic virus) et au virus de la mosaïque jaune zucchini (zucchini yellow mosaic virus), avec une homologie de la séquence des acides aminés de l'ordre de 74%. La résistance au PStV n'a pas été identifiée dans les cultivars commerciaux de l'arachide. Les stratégies de lutte contre les maladies sont examinées sur la base des informations épidémiologiques disponibles.

Resumen

Virus del estriado del maní. El virus del estriado del maní (peanut stripe virus, PStV) es un miembro del grupo potyvirus; se transmite mecánicamente, por áfidos (de manera no persistente) y por la semilla del maní (*Arachis hypogaea*). El PStV infecta naturalmente el maní en China, India, Indonesia, Malaisia, Myanmar, Filipinas, Tailandia, Estados Unidos y Vietnam. Distintos aislados del PStV inducen síntomas distintos en maní. En los Estados Unidos, es común el síntoma de estriado; sin embargo, en Asia de Sudeste, los síntomas más comunes son borrones de color verde oscuro y manchas anulares. Un buen hospedero de lesión local es *Chenopodium amaranticolor* y los hospederos de propagación son *Lupinus albus* y *Nicotiana benthamiana*. Se han producido antiseros para varios aislados del PStV y pruebas serológicas para detectar el virus en foliaje y semillas también están disponibles. A base de serología y el perfil peptídico de la proteína de la capa. El PStV se relaciona con el virus de mosaico del judía de vaca (blackeye cowpea mosaic virus). Se han iniciado estudios sobre la organización genómica del PStV al nivel molecular y la información hasta aquí conseguida sugiere que guarda relación con el virus de mosaico de soja (soybean mosaic virus), el virus de mosaico de sandía (watermelon mosaic virus) y el virus de mosaico amarillo zucchini (zucchini yellow mosaic virus) con una homología de secuencia de amino-ácidos de 74% aproximadamente. No se ha identificado resistencia a PStV en cultivares comerciales del maní. Basándose en la información existente, se han discutido estrategias del manejo de la enfermedad.

Cover and inside back cover: Nucleotide and deduced amino acid sequence of peanut stripe virus coat protein. (Source: Cassidy et al. 1993. Reprinted with permission from Springer-Verlag, Austria).

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Introduction

Numerous virus diseases have been reported infecting groundnut or peanut (*Arachis hypogaea* L.) in many countries. Many of these viruses belong to the potyvirus group with particle length between 680 and 900 nm, non-persistent aphid transmission, and virus-induced cylindrical/pinwheel inclusions in their hosts. Coat protein polypeptides of these viruses vary from 30 000 to 34 000 daltons, and their nucleic acid is a single-stranded (ss) RNA which varies from 3.0 to 3.3 million daltons. Potyviruses usually have an ultraviolet absorption ratio (260/280 nm) in the 1.14 to 1.25 range.

Xu et al. (1983) reported a potyvirus infecting groundnut in the Hubei province of the People's Republic of China that was named 'virus producing mild mottle' (VPMM). Demski et al. (1984) reported a potyvirus infecting groundnut in the USA that was named 'peanut stripe virus' (PStV). The USA virus originated in groundnut seed imported from China. Subsequent tests indicated that VPMM and PStV had a similar host range, could not be distinguished serologically and that both viruses were seed-transmitted in groundnut, suggesting that they were isolates of the same virus.

Since the virus disease caused by PStV posed a serious threat to groundnut production, a Peanut Stripe Virus Research Coordinators' Meeting was initiated and sponsored by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and the Peanut Collaborative Research Support Program (Peanut CRSP) supported by the United States Agency for International Development (USAID). It was held in June 1987 at the Malang Research Institute for Food Crops (MARIF), Indonesia, and one of the recommendations of the Meeting was that an information bulletin should be produced with emphasis on the identification of the virus and strategies for its control.

Distribution

After PStV was identified as a distinct virus in the early 1980s, subsequent surveys in groundnut-growing areas (Xu 1987; D.V.R. Reddy and J.W. Demski, unpublished), suggested that the virus was endemic in East Asia and Southeast Asia. Examination of a publication from Thailand (Choopanya 1973) suggests that the virus reported could have been an isolate of PStV. Likewise, Ting et al. (1972) presented data on a groundnut mosaic virus from Malaysia that could have been PStV. These viruses were earlier thought to have been the peanut mottle virus (PMV).

PStV is widely distributed in all groundnut-growing areas in China, but is most common in northern China, in the Shandong, Hubei, Henan, Liaoning, Jiangsu, and Anhui provinces where about 67% of the nation's total groundnuts are produced (Xu 1988). PStV was first reported in the USA by Demski et al. (1984), but serological tests on seed from earlier years' crops indicated that PStV was present in the country as early as 1979. PStV was first detected in India in 1987 (Prasada Rao et al. 1989), and is now widely distributed in the state of Gujarat. It occurs in all groundnut-growing areas of Indonesia, Malaysia, Myanmar, Philippines, Thailand, and Vietnam. The virus has also been detected in Japan and Senegal.

Symptoms

The name peanut stripe was given to the disease on the basis of stripes and green banding symptoms along lateral veins (Demski et al. 1984), characteristic of infected groundnut plants in the USA (Fig. 1). Subsequently, research on PStV obtained from different regions of the world indicated the existence of specific strains of the virus producing distinct symptoms on groundnut. The stripe isolate produces discontinuous stripes along the lat-

eral veins on young quadrifoliate; older leaflets show striping, mosaic in the form of green islands, and an oak leaf pattern (Fig. 2).

For most other PSTV isolates, the initial symptoms appear as chlorotic flecks (Fig. 3), followed by mild mottle, blotch, or chlorotic ring mottle symptoms (Fig. 4). Some isolates have been reported to produce leaf necrosis (Wongkaew and Dollet 1990).

PSTV differs from PMV in that the stripe symptoms persist in older leaflets, and early-infected plants are stunted in the case of isolates from Asia.

Causal Virus

Peanut stripe virus is a member of the potyvirus group and consists of filamentous flexuous rods, approximately 752 nm long and 12 nm in diameter (Fig. 5), which have a sedimentation coefficient of 150 S and a buoyant density in cesium chloride of 1.31 g cm⁻³. Each particle consists of a single protein species of 33 500 daltons. The genome is a single-stranded (ss) positive-sense RNA molecule of about 9500 nucleotides.

Virus Purification and Antiserum Production

It is difficult to purify PSTV from groundnut leaflets. Lupine (*Lupinus albus*), a crop adapted to temperate regions, is the most suitable host for purification. If lupine seed are not readily available or cannot be grown in greenhouses in tropical countries, infected leaves from kintoki bean (*Phaseolus vulgaris*), soybean (*Glycine max*; cv Yelredo or Bragg or any other susceptible cultivar) or *Nicotiana benthamiana* can be used.

Purification Procedure

The method given below was developed by Demski et al. (1984):

1. Collect lupine leaves with typical mosaic symptoms. In the case of other hosts, it is preferable to use leaves with initial symptoms.
2. Blend infected leaves in chilled, 0.1 molarity (M) Tris-HCl buffer (pH 8.0), containing 0.02 M sodium sulfite (Na₂SO₃) and 0.05 M disodium ethylenediaminetetraacetic acid. Use 3.0 mL of buffer for each gram of tissue.
3. Filter through two thicknesses of cheesecloth.
4. To the filtrate add cold chloroform to give 10% (V/V) and emulsify for 3–5 min.
5. Centrifuge at 4000 × g for 10 min at 5°C.
6. Collect the aqueous phase (upper clear layer).
7. Add sodium chloride (NaCl) to the aqueous phase to give 0.2 M, and polyethylene glycol (PEG, molecular weight 6000–8000) to give 4%. Stir at 4–6°C until NaCl and PEG are dissolved, then leave at 4–6°C for at least 90 min.
8. Collect the precipitate by centrifuging at 8000 × g for 10 min at 5°C.
9. Resuspend the precipitate in chilled 0.05 M borate-phosphate buffer (pH 8.3) containing 0.2 M urea (BPU).
10. Centrifuge at 4000 × g for 10 min at 5°C.
11. Layer the supernatant (25 mL) on a 13 mL column of 30% sucrose (in Beckman® SW 28 rotor tubes) prepared in BPU containing 4% PEG and 0.2 M NaCl. Centrifuge at 24 000 rpm for 2 h at 5°C.
12. Resuspend the pellets in BPU and centrifuge at 4000 × g for 10 min at 5°C.
13. Prepare density gradient columns by layering 6, 9, 9, and 9 mL of 10, 20, 30, and 40% sucrose, respectively, prepared in BPU in Beckman® SW 28 rotor tubes. Store the tubes overnight at 4–6°C.
14. Layer 8 mL of virus suspension from step 11 on each sucrose gradient and centrifuge at 24 000 rpm for 2 h at 5°C.
15. Collect the virus zone (located at 56–60 mm height from the bottom of the tube). *It may be necessary to perform another cycle of*

sucrose gradient centrifugation if the preparation contains host components.

16. Dilute the virus zone in 0.01 M phosphate buffer (pH 7.0) containing 0.85% NaCl (PBS) and centrifuge in a Beckman[®] R 40 rotor at 30 000 rpm for 2 h to pellet the virus.
17. Suspend the pellets in PBS (pH 7.2), and estimate the virus concentration spectrophotometrically by assuming an extinction coefficient of 3.0 ($E_{260nm}^{0.1\%} = 3.0$).

Production of Antiserum

Suspend 1.0 mg of purified virus in 1.0 mL of PBS (pH 7) containing 0.85% NaCl, with 1.0 mL of Freund's incomplete adjuvant. Obtain a thick emulsion by repeatedly drawing into a syringe and ejecting with force. Inject this emulsion intramuscularly into the hind leg of a rabbit (New Zealand White, inbred), preferably at three different sites, using approximately 0.3 mL at each site.

Give at least four injections at weekly intervals, and a fifth one if the antibody titre is low. Bleed the rabbit 2 weeks after the last injection. If the titre is high (over 1/600 as determined by the precipitin ring test), a rabbit can be bled 6–8 times at weekly intervals. Each bleeding usually yields 10–15 mL of serum. Lyophilize the serum in small portions (0.5–1.0 mL) and store at –70°C.

Disease Diagnosis

Diagnostic Hosts

Several potyviruses occur in groundnut, and for correct diagnosis it is essential to use only those hosts that can distinguish PStV. PMV often occurs in mixed infections with PStV; hosts that can be used to distinguish between the viruses are listed below:

Host	Peanut stripe virus	Peanut mottle virus
<i>Chenopodium amaranticolor</i>	Chlorotic or necrotic lesions	Majority of the isolates do not infect
Beans (<i>Phaseolus vulgaris</i>) cv Topcrop	No infection	Reddish-brown local lesions
Peas (<i>Pisum sativum</i>)	No infection	Systemic mosaic

PStV is readily transmissible mechanically from extracts prepared in 0.05 M phosphate buffer (pH 7.0) containing 0.01 M Na₂SO₃ or 0.2% thioglycerol.

Host Range

Susceptible natural hosts in the field are *Centrosema pubescens*, *C. macrocarpum*, *Calopogonium caeruleum*, *Crotalaria striata*, *Desmodium siliquosum*, and *Pueraria phaseoloides* (Wongkaew and Kantrong 1987). In the USA, PStV has been detected in *Desmodium* sp and *Indigofera* sp (Demski and Reddy 1988). Groundnut is commonly used for the maintenance of virus cultures. *Chenopodium amaranticolor* and *C. quinoa* are good local lesion hosts. Greenhouse tests showed PStV to have a relatively wide host range. The following plants were systemically infected by PStV after sap inoculation: *Astragalus sinicus*, *Cassia occidentalis*, *C. obtusifolia*, *Glycine max*, *Nicotiana glauca*, *Sesamum indicum*, *Trifolium incarnatum*, and *Trigonella foenum-graecum*.

The following test plants most frequently used for diagnosis were not infected by PStV: *Beta vulgaris*, *Brassica chinensis*, *Capsicum annuum*, *Crotalaria juncea*, *Cucumis sativus*, *Datura stramonium*, *Lablab purpureus*, *Hibiscus*

sabdariffa, *Lycopersicon esculentum*, *Pisum sativum*, *Sesbania cannabina*, *Melilotus albus*, *Medicago sativa*, *Nicandra physalodes*, *Nicotiana rustica*, *N. glutinosa*, *N. tabacum* (cv Xanthi), *Oscimum basilicum*, *Petunia angularis*, *P. hybrida*, *Phaseolus vulgaris* (cvs Royal Red, Topcrop, and Tamata), *P. mungo*, *P. limensis*, *P. lunatus*, *Physalis floridana*, *Spinacia oleracea*, *Trifolium hybridum*, *T. repens*, *T. pratense*, *Vicia faba*, *V. cracca*, *Vigna unguiculata* subsp *sesquipedalis* (cvs Hongzuiyan and Bailiaoxian), *V. sativa*, and *Zinnia elegans*.

Serology

PStV can be detected using enzyme-linked immunosorbent assay (ELISA) procedures that have been standardized at ICRISAT and the University of Georgia (Reddy et al. 1991).

All previously tested isolates of PStV had similar serological cross-reactions with a range of potyvirus antisera. In ELISA tests (both double antibody sandwich and direct antigen coating forms); all PStV isolates cross-reacted with antisera to blackeye cowpea mosaic virus (BICMV), soybean mosaic virus (SMV), clover yellow vein virus (CYVV) and adzuki bean mosaic virus (AzMV). Although peanut green mosaic virus (PGMV) also reacts strongly with antisera to BICMV, SMV, and AzMV, it is not known to react with CYVV antiserum (Sreenivasulu and Demski, in press). Since PGMV appears to be restricted to a few locations in India, it is unlikely to occur in mixed infections with PStV. None of the isolates of PStV tested so far cross-reacted with PMV antisera from various sources.

Transmission

PStV is transmitted by aphids in a nonpersistent manner (Demski et al. 1984, Camat 1985, Fukumoto et al. 1986). This is probably the only means by which the disease can spread from its primary source under field conditions.

Aphis craccivora, *A. gossypii*, and *Myzus persicae* have been tested for their transmission efficiency. With 10 viruliferous aphids per test plant and a 1–2 h acquisition access period, *A. craccivora* transmitted the virus at 90–100% frequency, while the frequency of *A. gossypii* was 33% (Camat 1985). Different symptom variants of PStV could have different aphid transmission frequencies. With two *A. craccivora* per plant (100 plants per variant), and acquisition and inoculation access periods of 2 min each, the mild mottle variant was transmitted to groundnut cv Tainan 9 at 10% frequency, while the ring spot and green blotch variants had frequencies of 7% and 3% respectively (S. Wongkaew, unpublished).

PStV transmission through groundnut seeds can be as high as 37% if the parent plants are artificially infected at an early age (Demski and Lovell 1985). However, seeds from naturally infected plants have lower seed transmission frequencies (0–7%) and this is highly variable from plant to plant. Most cultivars tested showed less than 4% seed transmission (Xu et al. 1983, Demski and Reddy 1988, S. Wongkaew, unpublished). Seed transmission frequency is probably influenced by environmental conditions, virus isolate, and the groundnut cultivar used.

The virus can be detected in both the embryo axis and the cotyledon. A technique has been developed for the detection of PStV in individual seeds without affecting their germination (Demski and Warwick 1986). ELISA can detect one PStV-infected seed in a pool of 25 healthy samples. A dot blot hybridization technique has also been applied to detect PStV in seeds. The sensitivity of this technique is about 10 times greater than ELISA (Bijaisoradat and Kuhn 1988). Further, the technique can differentiate between the presence of PStV and PMV in groundnut seeds.

Inclusions

A method described by Christie (1967) can be employed to observe the virus inclusions with

a compound light microscope. Although the epidermal layer on either side of the leaf can be used, the abaxial side is preferable. The detached epidermal layer is immersed in a 2.5% Triton[®] X-100 solution for 2–3 min to remove chloroplasts and then transferred to distilled water to wash off the Triton[®] X-100. The tissue is left to float on water for 1–2 min and is then mounted in 0.05% toluidine blue-0 in 0.05 M potassium phosphate buffer (pH 7.0). The inclusion bodies induced by stripe, blotch, and mild mottle isolates of PStV are similar (Fig. 6).

For ultrathin sections, a small piece of a diseased leaf is fixed in 2% glutaraldehyde in a 0.1 M sodium phosphate buffer (pH 7.0) for 30 min, then postfixed in 1% osmium tetroxide in the same buffer. Samples can be dehydrated by an ethanol series and mounted in Spurr resin. Ultrathin sections are stained with uranyl acetate and lead citrate and examined with an electron microscope. In ultrathin sections of diseased groundnut leaves, pinwheel and bundle type inclusion bodies typical of potyviruses are observed in the cytoplasm of the infected cells.

Virus Particles

Virus particles can be examined by electron microscopy using leaf dip and purified virus preparations. Dip preparations are made by grinding a small piece of a diseased leaf in 2–3 drops of 2% phosphotungstate (pH 6.5), and mounting the extract on a carbon-stabilized, Formvar[®]-coated grid. The purified virus is mixed with an equal volume of 4% potassium phosphotungstate (pH 6.5), and a drop of this mixture is placed on a carbon-stabilized, Formvar[®]-coated grid. Particles can also be stained with 2% uranyl acetate. Both methods showed filamentous flexuous particles, most of which were 12 nm wide and 752 nm long (Fig. 5).

Peptide Profiling of Coat Protein

High performance liquid chromatography (HPLC) peptide profiling of potyvirus coat protein digests has recently been shown to be a very useful approach to differentiate between potyviruses and their strains (Shukla et al. 1988). This procedure reflects the extent of amino acid sequence identity between coat proteins of potyviruses and has facilitated classification of strains of potyviruses into various subgroups (Ward and Shukla 1991). The approach has revealed that the potyvirus isolates inducing different symptoms in groundnut—blotch, stripe, mild mottle, and necrosis—are strains of PStV (Kittipakorn et al. in press). AzMV, BICMV, PStV, and three soybean potyvirus isolates from Taiwan resemble (in their peptide profiles) viruses in serogroup 'B' of bean common mosaic virus (BCMV) (McKern et al. 1991, 1992a, 1992b). A comparison of the amino acid sequences of the coat protein of the PStV stripe isolates with that of a strain of BCMV (BCMV-NL₄-serogroup B) further confirmed the above results. These two viruses exhibit a coat protein sequence identity of approximately 90% (McKern et al. 1992b), a level of identity generally observed among the strains of the same potyvirus (Ward and Shukla 1991). The name 'bean common mosaic virus' has been proposed for AzMV, BICMV, PStV, and the soybean potyvirus isolates PM, PN, and 74, since BCMV was reported earlier than these viruses (McKern et al. 1992b). However, on the basis of this information alone, we do not think it is advisable at this stage to include PStV among BCMV strains. Although two soybean isolates of BCMV from Taiwan were shown to infect groundnuts, major differences in host range indeed exist between isolates of BCMV and PStV. Moreover, the morphology of cytoplasmic inclusion bodies of PStV (currently included under subdivision IV) differs from that of BCMV (included under subdivision II). Therefore, PStV will continue to be regarded as a distinct potyvirus until additional data on

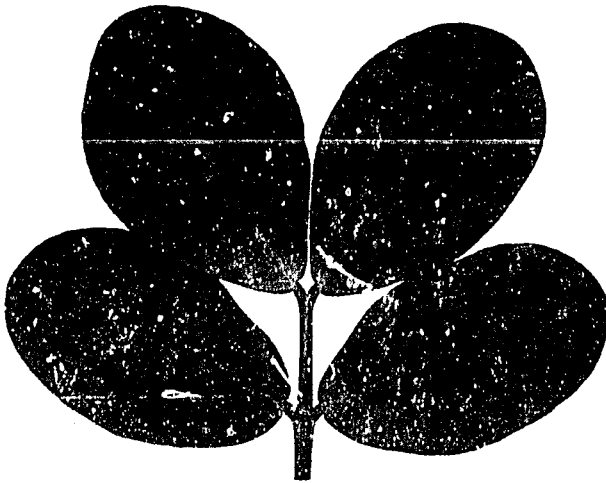


Figure 1. Stripe and green banding symptoms along lateral veins of groundnut leaflets.



Figure 2. Older leaflets of groundnut showing striping and mosaic in the form of green islands and an oak leaf pattern.

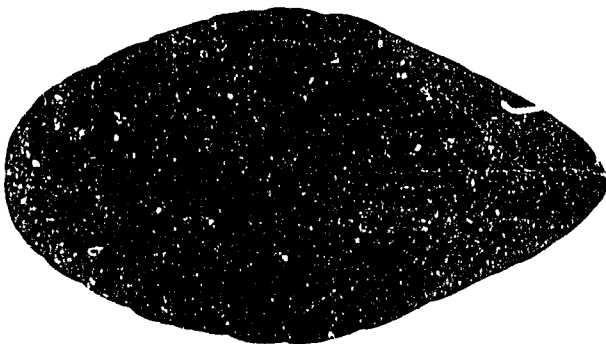


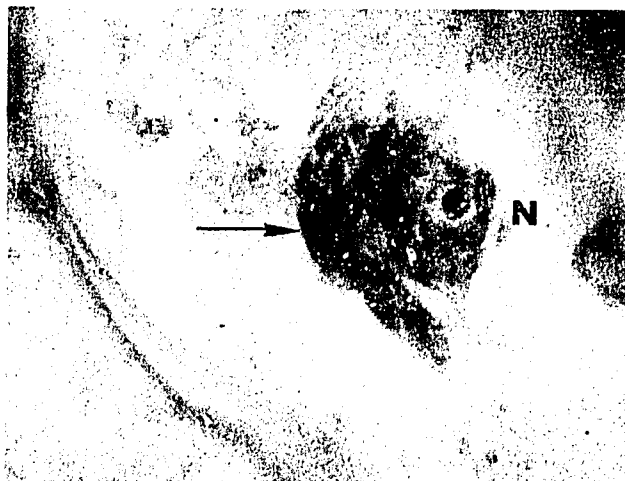
Figure 3. Chlorotic flecks on groundnut leaflet.

Figure 4. Chlorotic ring mottle symptoms on groundnut leaflets.



Figure 5. Electron micrograph of a purified peanut stripe virus preparation ($\times 257\ 000$).

Figure 6. A subdivision-IV type inclusion body (arrow) adjacent to the nucleus (N) produced in a PSIV-infected groundnut leaflet ($\times 1940$) (Photo courtesy: R. Christie, University of Florida, USA).



biological and molecular properties are obtained.

PStV Genome Organization

In the case of potyviruses in general, genomic RNA encodes for a large precursor polyprotein which is subsequently processed into nine mature proteins by several virus-encoded proteinases (Riechmann et al. 1992). PStV genome also encodes for a large precursor polyprotein. The nucleotide sequence of a 'blotch' isolate of PStV (obtained from J.W. Demski) is currently being determined (B.G. Cassidy and U.B. Gunasinghe, unpublished). From the sequence information obtained to date, the order of mature proteins predicted within the approximately 9.5 kb RNA is the same as that of the other cloned and sequenced potyviruses (Riechmann et al. 1992). The genome organization is shown in Figure 7.

The potyvirus genome comprises a single RNA of 9.5 kb which contains a 5'-terminal genome-linked protein (VPg) and a 3'-terminal poly-A tail. The N-terminal protein (P1) has been shown to possess a self-processing proteinase activity (Verchot et al. 1991) and has been suggested to be involved in virus cell-to-cell movement (Domier et al. 1987). The helper component-protease has a self-processing proteinase activity at its carboxyl end, whereas the helper component has been shown as essential for aphid transmissibility. The P3 (cylindrical inclusion and 6K proteins)

have been speculated to be involved in regulation of proteinase processing and replication. The nuclear inclusion *protein a* contains two functional domains. The carboxyl half encodes for a proteinase responsible for the majority of the polyproteins proteinase processing (Parks and Dougherty 1991). The amino terminal half encodes for the VPg protein. The nuclear inclusion *protein b* is believed to be the viral RNA-dependent RNA polymerase because of its high degree of identity to other replicases and contains the highly conserved motif GXXXTXXXN(X)₂₀₋₄₀ GDD found in almost all known RNA-dependent RNA polymerases (Kamer and Argos 1984). The coat protein (CP) is coded by the 3' most region of the RNA genome *c* and is responsible for structurally encapsidating the PStV viral RNA genome (Cassidy et al. 1993).

The sequence of the entire PStV genome is yet to be determined. Data obtained to date indicate that PStV is closely related to SMV, water melon mosaic virus, and zucchini yellow mosaic virus. Each of these shares a 74% amino acid sequence identity with PStV.

Disease Cycle

The source of primary PStV inoculum appears to be infected groundnut seed with subsequent dissemination by aphids. Although several weed hosts in Thailand gave positive serological results with PStV antiserum, their contribution to virus spread is unknown. In

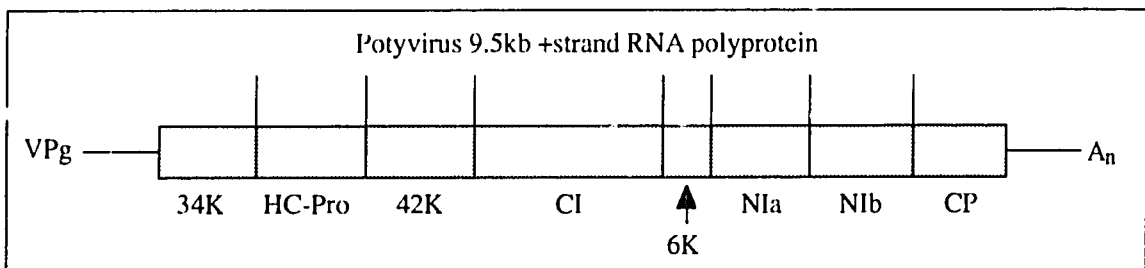


Figure 7. Peanut stripe virus genome organization.

the USA, PStV incidence in groundnut was high (over 50%) for two consecutive years in a field research plot. Virus-free groundnut seeds were sown in the same plot in the third year, and the resulting crop was virus-free throughout the year. This suggests that the presence of PStV in groundnut may not necessarily lead to virus establishment in weed hosts.

Studies have indicated that the distance of PStV spread from a virus source is relatively short. In the USA, PStV did not infect healthy groundnut plants that were isolated by a bare soil strip of 83 m from infected groundnut plants. Virus infection in the USA did not occur in five groundnut fields sown 100 m from a PStV source. In 1985, in Wuhan, China, virus-free seed were sown in commercial fields and in other plots 100 and 200 m from the commercial groundnut fields. Nearly all plants (97%) from virus-free seed became infected in the commercial fields but only 15% were infected when plants were 100 m away, and no infection was observed at 200 m distance. Similar results were obtained in Xuchou, China, where virus-free seed were sown in commercial fields and in plots 50 m away from farmers' fields.

Disease Management

Resistance

Cultivation of resistant cultivars would be the most reliable method for PStV management, but resistance to PStV has not yet been found in the cultivated groundnut. In a study in the USA, 20 groundnut cultivars commonly grown in the country and 224 plant introductions were infected by PStV (Demski and Reddy 1988). Approximately 10 000 accessions from ICRISAT's groundnut germplasm bank were evaluated for resistance to PStV in Indonesia. Some plants of all accessions developed symptoms, but some lines showed only mild symptoms. In some cases, symptoms were de-

layed until late in the growing season (Saleh et al. 1989). In Thailand, genotypes which were either tolerant to PMV or had low PMV seed transmission frequency were severely diseased by PStV (Wongkaew et al. 1988). Another approach is to develop groundnut cultivars with very little or no seed transmission. This control strategy would reduce both sources of primary inoculum and subsequent secondary spread of PStV by aphid vectors.

Virus-free Seed

Many groundnut crops in areas where the PStV disease is established, have a high virus incidence and probably some infected seed at harvest. Seed transmission of 2-5% is sufficient to lead to an epidemic (Demski and Reddy 1988). The common practice of farmers using seed from the previous season's crop assures high PStV incidence because of the omnipresence of aphid vectors. Therefore, production and distribution of virus-free seed should be given a high priority.

Tests in Thailand and China indicated that some groundnut genotypes had seed transmission frequencies of <1% while others had frequencies of over 10%. Priority should be given to screening groundnut germplasm for resistance to PStV seed transmission. The seed transmission frequency of PStV has sometimes been correlated with the size of groundnut seeds, with higher frequencies in small seeds. Selection of large seeds for sowing could reduce the source of primary inoculum and thus decrease the incidence of disease.

Cultural Practices

Since infected plants act as a source of PStV inoculum for further spread, roguing of such plants could be expected to reduce virus incidence. Unfortunately, this procedure has not been successful in controlling diseases induced by potyviruses (Demski et al. 1984). By

the time the symptoms develop and plants are recognized as being infected with PStV, the aphids could often have transmitted the virus to other plants. Moreover, roguing is not practical for large crop areas.

The date of sowing, spatial isolation, crop rotation, plant spacing, and reflective mulching might have an influence on the spread of PStV, but further research is needed to determine the effects and practicability of these cultural practices on PStV incidence.

Vector Control

PStV is transmitted by *Aphis craccivora*, *A. gossypii*, and *Myzus persicae*, and probably by many other aphid species, in a nonpersistent manner. Pesticides could be applied to decrease the vector population. However, low population densities that are not directly harmful to crops could still be effective in virus dissemination, especially in the case of nonpersistently transmitted viruses dispersed by noncolonizing aphids while probing on plants in search of a suitable host plant. Insecticides usually do not kill aphids fast enough or reduce population sufficiently to prevent virus spread in the field. Attempts to control PStV by using a 1% milk suspension, oxydemeton methyl (Metasystox[®]), or milk alternated with Metasystox[®] or pyrimidine carbamate (systemic aphicide) were ineffective, and even appeared to increase the rate of virus spread (Wongkaew et al. 1988).

Other Strategies

Plant quarantine stations should develop expertise and facilities to detect PStV in plant material including seed. Adoption of quarantine and inspection measures to prevent further spread of PStV into countries or geographical areas which are now PStV-free are warranted. It may be necessary to restrict the export of groundnut seed from areas

where PStV is prevalent. Even the movement of infected seed within a state or country could be important. In southern China, farmers prefer growing spanish type groundnut cultivars released from local research institutes or extension services. They do not grow the virginia type normally cultivated in northern China where PStV is prevalent. We recommend strict quarantine regulations, especially in countries where PStV is known to be restricted to certain locations. These should include:

- No distribution of seed from PStV-infested areas.
- Seed lots (germplasm, breeders seed, etc.) for experimental purposes should be tested by the nondestructive ELISA method prior to their distribution to noninfested areas.
- Only PStV-free seed should be used for sowing in infested areas. Sowing in the proximity of leguminous crops or other potential hosts of PStV should be avoided.
- Thorough surveys to detect possible occurrence of PStV in other crop plants and weeds, especially in perennial weeds, should be undertaken. This would help eliminate weed hosts and avoid crops that are highly susceptible to PStV.

In general, application of plastic film mulch in groundnut fields enhances groundnut growth and increases yield. Field trials in China showed that this also reduced PStV disease incidence.

Production of Transgenic Plants with PStV Genes

Efforts are under way to induce resistance to PStV by incorporating the virus coat protein gene into the groundnut genome. The resulting transgenic groundnuts could lead to the development of cultivars with resistance to PStV.

Although resistance to PStV has been identified in some wild *Arachis* species (Culver et al. 1987, Prasada Rao et al. 1991), no attempts have been made to transfer this resistance to *A. hypogaea*; this should be given high priority.

Conclusions

A great deal has been learned about PStV in the 10 years since it was recognized as a distinct virus. It has been fully characterized, and specific strains have been found that differ in symptom expression, disease severity, and degree of seed transmission. Antisera have been produced, and research and plant quarantine workers in many countries are now able to detect and diagnose PStV in infected groundnut plants and seed. Limited research on the vector system has highlighted the role of *Aphis craccivora* in the spread of the disease. The availability of improved diagnostic tools for PStV should facilitate research on the vectors, and this should result in better control measures. It is unlikely that useful levels of resistance to PStV will be found in the cultivated groundnut, and attention is being focused on the identification of genes from wild *Arachis* species and the use of genetic engineering techniques to produce transgenic groundnut plants expressing resistance to the virus. If successful, these approaches could result in breeding of PStV-resistant cultivars which would be important components in future integrated disease management systems.

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