A Potyvirus Causing Mosaic Disease of Sesame (*Sesamum indicum*)

P. SREENIVASULU, Visiting Professor, and J. W. DEMSKI, Professor, Department of Plant Pathology, University of Georgia, Georgia Experiment Station, Griffin 30223; D. E. PURCIFULL, Professor, Department of Plant Pathology, and R. G. CHRISTIE, Senior Biological Scientist, Department of Agronomy, University of Florida, Gainesville 32611; and G. R. LOVELL, Chief Curator, U.S. Department of Agriculture, Regional Plant Introduction Station, Georgia Experiment Station, Griffin 30223

ABSTRACT

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A virus causing chlorosis of veins, mosaic, green banding along veins, and downward leaf rolling in sesame (*Sesamum indicum*) was isolated from sesame plants grown from seed imported from the Sudan. The virus was sap-transmissible to species of Amaranthaceae, Chenopodiaceae, Cucurbitaceae, Leguminosae, and Solanaceae. *Chenopodium amaranticolor* was used as a local lesion assay host and *Pisum sativum* cv. Little Marvel, as the propagation host for purification. The virus was nonpersistently transmitted by *Aphis craccivora* and *Myzus persicae* but was not transmitted through the seed of sesame. The virus remained infective in buffered leaf sap of *Nicotiana benthamiana* at a dilution of 10^{-5} after storage for 9 days at 25 C and heating for 10 min to 55 C (but not to 60 C). The virus induced cylindrical cytoplasmic inclusions in infected tissues of *Lupinus albus*. Purified virus preparations yielded flexuous filamentous particles that contained a major polypeptide of approximately 33 kDa and one nucleic acid species with molecular weight of 3.1×10^6. In indirect enzyme-linked immunosorbent assay, the virus reacted positively to antisera of blackeye cowpea mosaic, peanut green mosaic, peanut stripe, pea seedborne mosaic, soybean mosaic, tobacco etch, watermelon mosaic virus 2, and zucchini yellow mosaic viruses but not to watermelon mosaic virus 1 and peanut mottle and bean common mosaic viruses. In reciprocal tests, peanut stripe virus and watermelon mosaic virus 2, but not peanut green mosaic, peanut mottle, pea seedborne mosaic, blackeye cowpea mosaic, soybean mosaic, and tobacco etch viruses, reacted with the antiserum for the sesame virus. On the basis of these properties, the causal virus is identified as an unnamed potyvirus isolate causing sesame mosaic.

Sesame (*Sesamum indicum* L.) is grown as an oilseed crop in tropical and subtropical parts of the world (29). Kolte (12) described the various diseases of sesame caused by different pathogens and described the common virus diseases of sesame as mosaic and leaf curl. Potyviruses naturally infecting sesame are watermelon mosaic virus (WMV) found only in Korea (4), a virus related to blackeye cowpea mosaic (BlCMV) in Brazil (14), and a virus from China that may be related to peanut stripe (PStV) (30,31). Reports of viruses infecting sesame in North America could not be found, although PStV was isolated from sesame growing adjacent to peanut (*Arachis hypogaea* L.) infected with PStV (J. W. Demski, *unpublished*). Viruses reported to infect experimentally inoculated sesame are peanut green mosaic (26), cowpea mild mottle (27), cucumber mosaic (5), tobacco and tomato ringspot (18), and peanut mottle (25). Sesame was also used as an indicator host in the identification of citrus dwarf and potato X viruses (3,11).

Present address of first author: Department of Virology, S. V. University, Tirupati-517502, A.P., India.

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In 1986, over 50% of the sesame plants grown in a 0.2-ha field sown in Spalding County, Georgia, showed unknown virus symptoms. Preliminary tests indicated that the virus was a potyvirus but was not PStV. In this paper, we describe the biological, physical, biochemical, and serological properties of the virus causing mosaic disease of sesame in Georgia.

MATERIALS AND METHODS

Virus culture and maintenance. Samples of virus-infected sesame were collected from USDA Plant Introduction plots (Georgia Experiment Station, Griffin). Virus was extracted from infected tissues in 0.05 M potassium phosphate buffer, pH 7.0, containing 0.1% 2-mercaptoethanol and mechanically inoculated in the greenhouse to sesame and *Chenopodium amaranticolor* Coste & Reyn. Virus was isolated from a single lesion on *C. amaranticolor* and propagated in sesame, *Nicotiana benthamiana* Domin., pea (*Pisum sativum* L. cv. Little Marvel), and squash (*Cucurbita pepo* var. *melopepo* (L.) Alef.).

Host range. Six to 10 plants of each test species or cultivar (Table 1) were mechanically inoculated with sap from *P. sativum*, and 3–4 wk later, both the inoculated and newly developed leaves were tested for virus by enzyme-linked immunosorbent assay (ELISA) and/or back-inoculation to *C. amaranticolor*.

Properties in sap. The dilution end point, thermal inactivation point, and longevity in vitro of the virus were determined using sap from infected *N. benthamiana*. The thermal inactivation point was determined at 5° increments from 40 to 80 C, and treated sap was inoculated on *C. amaranticolor*.

Aphid transmission. Colonies of *Aphis craccivora* Koch and *Myzus persicae* (Sulzer) were maintained on cowpea (*Vigna unguiculata* (L.) Walp. subsp. *unguiculata* cv. California Blackeye) and pepper (*Capsicum annuum* L.), respectively. Aphids were starved 14–16 hr in glass vials and then given a 2-min acquisition access period on virus-infected detached young sesame leaves. Aphids were then transferred to healthy sesame test plants (two aphids per plant) and given a 1–2 hr inoculation access period. Test plants were sprayed with malathion to kill the aphids, then transferred to the

Table 1. Host range of the sesame virus isolate

Species	Reaction[a]
Chenopodium amaranticolor	NLL
Citrullus lanatus	SCS, SM
Cucurbita pepo var. *melopepo*	SCS, SM, SVC
C. pepo cv. Small Sugar	SCS, SM, SVC
Cyamposis tetragonoloba	NLL
Glycine max	
cv. Bragg	LR, NLL, SVN
cv. Davis	NLL, SVN
Gomphrena globosa	LSI
Lupinus albus	SCS, SM
Nicotiana benthamiana	LD, SM
N. clevelandii	SCS, SM
N. tabacum cv. Burley 21	CLL
Petunia × *hybrida*	LSI
Phaseolus vulgaris cv. Pinto	NLL
Pisum sativum	
cvs. Little Marvel and Alaska	CLL, SCS, SM
Sesamum indicum	CLL, GB, LR, SM, SVC
Trifolium incarnatum	GB, SM, SVC
Vigna unguiculata subsp. *unguiculata* cv. California Blackeye	CLL, GB, LD, SM

[a] CLL = chlorotic local lesions, GB = green bands along lateral veins, LD = leaf deformation, LR = leaf rolling, LSI = local symptomless infection, NLL = necrotic local lesions, SCS = systemic chlorotic spotting, SM = systemic mosaic, SVC = systemic veinal chlorosis/vein clearing, SVN = systemic veinal necrosis.

greenhouse, where they were observed for visual symptoms and tested for virus by ELISA.

Seed transmission. Seven hundred residual seed of the original sesame imported from the Sudan and 1,200 harvested seed from infected plants grown in the Georgia plots were sown in trays of steam-sterilized soil in the greenhouse. Six weeks after sowing, groups of six seedlings were tested for virus by ELISA.

Virus purification. The procedure adopted for the purification of the virus was similar to method one of Reddick and Barnett (22). Virus-infected leaves of Little Marvel pea were homogenized in a Waring blender in 0.5 M potassium phosphate buffer, pH 7.0, containing 1.0 M urea, 0.02 M disodium ethylenediaminetetraacetic acid, 0.01 M sodium diethyldithiocarbamate, and 0.5% thioglycerol at the rate of 3.0 ml/g of tissue. Final virus pellets were resuspended in 0.05 M potassium phosphate buffer, pH 7.0, containing 0.85% NaCl (for immunizing a rabbit), in sample buffer (for molecular weight determination of virus protein) or in sterile 0.05 M potassium phosphate buffer, pH 7.0 (for virus nucleic acid extraction).

Molecular weight determinations. The molecular weight of the virus polypeptide was determined by the method of Laemmli (13) as described by Reddy and Black (23). Protein bands were stained with Coomassie brilliant blue R-250 as described by Reddy and Macleod (24), and distance migration for each polypeptide band was measured for calculating the molecular weight of virus polypeptide.

RNA from purified virus was isolated as previously described (17,28). Tobacco mosaic virus RNA (molecular weight 2.0×10^6) and *Escherichia coli* ribosomal RNAs (molecular weights 1.1×10^6 and 0.56×10^6) were used as markers for calculating the relative molecular weight of viral RNA. The viral and marker RNAs were denatured in a medium containing 70% dimethyl sulfoxide in electrolyte buffer (v/v). Samples were heated at 50 C for 10 min and cooled quickly in ice water. Electrophoresis of denatured RNAs was performed according to the method of Loening (16) in 2.4% polyacrylamide tube gels (0.5×11 cm) containing 0.2% sodium dodecyl sulfate (SDS) (w/v). Gels were subjected to a constant current of 6 mA per tube for 4–5 hr, fixed overnight in a mixture of ethanol:glacial acetic acid:distilled water (40:10:50, v/v), and scanned with an ISCO Model UA-5 absorbance monitor.

Serology. The virus suspension was emulsified with an equal volume of Freund's incomplete adjuvant and injected intramuscularly into a rabbit at weekly intervals (average of 3.4 mg per injection). The rabbit was bled 2 wk after the fifth injection and thereafter at weekly intervals for 6 wk.

The titer of the serum was determined by the precipitin ring test (1) using purified virus and by indirect ELISA with virus-infected pea leaf extract as antigen (described below). The double-antibody sandwich ELISA (DAS-ELISA) employed for detecting the virus was similar to that described by Lister (15) and Rajeshwari et al (21), with the exception that the antigen buffer contained 0.025 M phosphate and 0.1 M Na_2 EDTA. The antiviral immunoglobulins, purified by $(NH_4)_2SO_4$ precipitation, were used at 1 μg/ml for coating antibody, and the enzyme conjugate was used at 1/1,000 dilution. The indirect ELISA procedure, for serum titer determination and for studying serological relationships of the sesame virus with other potyviruses, was similar to direct antigen coating ELISA (DAC-ELISA) and plate-trapped antigen ELISA (PTA-ELISA) described by Hobbs et al (8) and Mowat and Dawson (19), respectively. Protein A-alkaline phosphatase conjugate (P 9650, Sigma, St. Louis, MO) at 0.1 unit per milliliter of conjugate buffer was used to detect the antigen-antibody reaction. The plates with antigens and crude antisera were incubated for 1 hr at 37 C and those with protein A-alkaline phosphatase, for 90 min at 37 C. Substrate, *p*-nitrophenyl phosphate at 1 mg/ml of substrate buffer, was incubated at room temperature (25 C) for 2 hr. Reactions were stopped by adding 50 μl of 3.0 M NaOH to each well, and the plates were read in a Dynatech Minireader II at 410 nm.

The antisera (1/1,000 dilution) used were to BlCMV, PStV, watermelon mosaic virus 2 (WMV-2), watermelon mosaic virus 1 (WMV-1), zucchini yellow mosaic virus (ZYMV), soybean mosaic virus (SMV), peanut mottle virus (PMV), peanut green mosaic virus (PGMV), pea seedborne mosaic virus (PSBMV), tobacco etch virus (TEV), and bean common mosaic virus (BCMV NL-15). The viruses used in the indirect ELISA were propagated as follows: sesame isolate and WMV-2 in *S. indicum*, PMV and PSBMV in *P. sativum* cv. Little Marvel, PStV in *Lupinus albus* L., PGMV in *N. benthamiana* and *A. hypogaea*, TEV in *Nicotiana tabacum* L. cv. Burley 21, BlCMV in *V. unguiculata*, and SMV in *Glycine max* (L.) Merr. cv. Bragg.

Serological relationships of the sesame virus, WMV-2, and PStV were also investigated by immunodiffusion tests (20) in agar gels containing 0.8% Noble agar, 0.5% SDS, and 1.0% sodium azide. Antigens consisted of SDS-treated extracts (1 ml of water and 1 ml of 3% SDS per gram of tissue) from infected or healthy *N. benthamiana* plants. Antisera were used undiluted.

Light and electron microscopy. Viral inclusion bodies in white lupine and cowpea epidermal tissues were prepared, stained, and examined by light microscopy as described by Christie and Edwardson (6). Virus for particle determination was obtained from pea leaves by the procedure of Christie et al (7), stained with 2.0% aqueous uranyl acetate, and examined in a Zeiss EM IOA electron microscope.

RESULTS

Symptoms on sesame. The symptoms on sap-inoculated sesame leaves were chlorotic spots and on systematically infected leaves, veinal chlorosis, mosaic, dark green veinbanding along lateral veins, and downward rolling of leaf margins. Leaf size and whole plant size were reduced compared with healthy plants.

Host range. Plants infected by the virus are listed in Table 1. *C. amaranticolor, Cyamopsis tetragonoloba* (L.) Taub., *N. tabacum* cv. Burley 21, and *Phaseolus vulgaris* L. cv. Pinto showed only local lesions. *Citrullus lanatus* (Thunb.) Matsum. & Nakai, *C. p. melopepo, C. pepo* cv. Small Sugar, *L. albus, N. benthamiana, Nicotiana clevelandii* A. Gray, and *Trifolium incarnatum* L. showed systemic symptoms. *G. max* cvs. Bragg and Davis, *P. sativum* cvs. Little Marvel and Alaska, and *V. u. unguiculata* cv. California Blackeye reacted with both local and systemic symptoms. *Gomphrena globosa* L. and *Petunia* × *hybrida* Hort. Vilm.-Andr. were locally infected but without visible symptoms.

Plants not infected and from which no virus was recovered were *A. hypogaea* cv. Florunner, *C. annuum, Cucumis melo* L., *C. sativus* L., *Cucurbita moschata* (Duchesne) Duchesne ex Poir., *Datura stramonium* L., *Luffa acutangula* (L.) Roxb., *Lycopersicon esculentum* Mill., *Medicago sativa* L., *Nicotiana glutinosa* L., *P. vulgaris* cv. Topcrop, *V. unguiculata* cv. Clay, and *Vinca rosea* L.

Properties in sap. The dilution end point of the virus was between 10^{-5} and 10^{-6}, the thermal inactivation point was between 55 and 60 C, and longevity in vitro was between 9 and 10 days at 25 C.

Aphid transmission. Both *A. craccivora* and *M. persicae* transmitted the virus in a nonpersistent manner. After a 2-min acquisition access period, *A. craccivora* transmitted the virus to five of 41 sesame plants, and *M. persicae* transmitted the virus to 17 of 41 sesame plants. All symptomatic plants were virus-infected, as verified by DAS-ELISA.

Seed transmission. The 1,649 sesame plants grown from original and increased seed exhibited no external symptoms. No virus was detected by DAS-ELISA in 740 random samples of these plants.

Virus purification. The purification procedure consistently yielded 20–50 mg (assuming an extinction coefficient of 3.0) of virus from 1 kg of pea leaves. Purified virus was infective on sesame and *C. amaranticolor*. The ultraviolet

absorption spectrum of the purified virus had a shoulder at 290 nm, and the A_{260}/A_{280} was 1.29. The A_{260}/A_{245} was 1.10. ELISA tests using antiserum prepared to the purified virus did not give reactions to sap of healthy plants.

Molecular weight determinations. Viral protein preparations contained a major polypeptide of approximately 33 kDa and a minor polypeptide of approximately 29 kDa (Fig. 1). Viral nucleic acid, assumed to be RNA, migrated as a single band with an estimated molecular weight of 3.1×10^6.

Serology. The titer of the antiserum was 1/1,024 by precipitin ring test and 1/80,000 by indirect ELISA. In indirect ELISA, this virus cross-reacted strongly with antisera to WMV-2, SMV, and PSBMV; moderately with antisera to BlCMV, PGMV, PStV, TEV, and ZYMV; and very weakly with antiserum to PMV (Table 2). It did not react with antisera to BCMV NL-15 and WMV-1 (Table 2). On the other hand, WMV-2 cross-reacted strongly with antisera to BlCMV, PGMV, PSBMV, PStV, SMV, and TEV; moderately with antiserum to the sesame isolate; and weakly with antisera to PMV and WMV-1. WMV-2 did not react with BCMV NL-15 antiserum. In reciprocal tests, only PStV antigen reacted moderately against the sesame isolate antiserum. Antigens of BlCMV, PGMV, PSBMV, SMV, PMV, and TEV did not react or reacted very weakly with antisera to the sesame isolate (Table 3). All these viral antigens reacted strongly against antiserum to WMV-2.

In immunodiffusion tests, the sesame virus was antigenically related to, but different from, both WMV-2 and PStV (Fig. 2). The sesame virus antiserum reacted weakly with WMV-2 and PStV in four of five tests, resulting in reactions of partial identity. One antiserum to WMV-2 reacted very weakly with the sesame virus in one of six tests but negatively in five other tests. The PStV antigen reacted with this WMV-2 antiserum in six of six tests. A second WMV-2 antiserum was tested twice, and it cross-reacted with PStV but not with the sesame virus. The PStV antiserum cross-reacted with both WMV-2 and the sesame virus in each of seven tests. In all cases where cross-reactivities were observed, homologous precipitin bands formed spurs over heterologous precipitin bands (Fig. 2). Antiserum to PStV cross-reacted with both WMV-2 and the sesame virus in each of seven tests, with the band formed by PStV spurring over the bands by either WMV-2 or the sesame virus (Fig. 2).

Light microscopy. Cylindrical inclu-

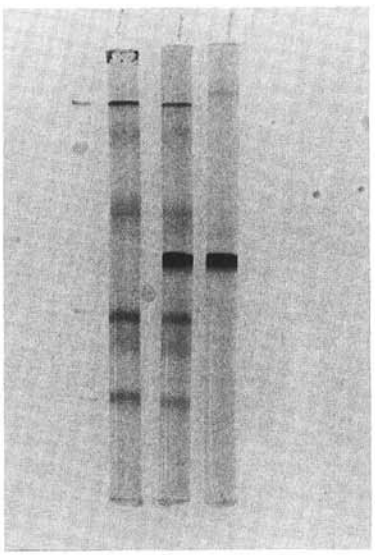

Fig. 1. The sesame isolate virus contains a major polypeptide of 33×10^3 daltons and a minor polypeptide of 29×10^3 daltons. Left lane = marker proteins, center lane = marker proteins and sesame isolate, and right lane = sesame isolate. Molecular weights of marker proteins were bovine plasma 66,000, egg albumin 45,000, pepsin 34,700, trypsinogen 24,000, β-lactoglobulin 18,400, and lyzozyme 14,300.

Table 2. Absorbance values for the sesame isolate and watermelon mosaic virus 2 (WMV-2) with 12 potyvirus antisera in indirect ELISA

	Antigens[b] (10^{-1})			
Antisera[a]	Sesame isolate	WMV-2	Healthy control	Virus control
Sesame isolate	1.86	0.79	0.00	...
WMV-2	1.90	1.94	0.00	...
BCMV NL-15	0.00	0.00	0.00	NA[c]
BlCMV	0.71	1.20	0.00	1.40
PGMV	0.59	1.82	0.02	1.72
PMV	0.22	0.34	0.00	1.19
PSBMV	1.48	1.86	0.00	1.77
PStV	0.90	1.56	0.00	1.85
SMV	1.63	1.90	0.00	1.83
TEV	0.56	1.16	0.00	1.84
WMV-1	0.02	0.28	0.00	NA
ZYMV	0.82	1.82	0.00	NA

[a] Crude antisera used at 1:1,000 dilution.
[b] Leaf tissue extracted at 1 g per 9 ml of antigen extraction buffer = 10^{-1} dilution. Values (A_{410}) represent average of two replications. All values are the readings above healthy controls, which served as the base reading.
[c] NA = homologous antigens not available.

Table 3. Reactions of seven potyviruses with antisera to the sesame isolate and watermelon mosaic virus 2 (WMV-2) in indirect ELISA

		Antisera[b]	
Antigens	Antigen dilutions[a]	Sesame isolate	WMV-2
Viruses			
BlCMV	10^{-1}	0.17	1.50
	10^{-2}	0.32	1.65
	10^{-3}	0.17	1.51
PGMV	10^{-1}	0.11	1.71
	10^{-2}	0.08	1.66
	10^{-3}	0.05	1.48
PMV	10^{-1}	0.15	0.68
	10^{-2}	0.14	0.57
	10^{-3}	0.16	0.49
PSBMV	10^{-1}	0.07	1.55
	10^{-2}	0.14	0.83
	10^{-3}	0.25	1.09
PStV	10^{-1}	0.68	1.69
	10^{-2}	0.72	1.73
	10^{-3}	0.70	1.70
SMV	10^{-1}	0.20	1.69
	10^{-2}	0.23	1.68
	10^{-3}	0.24	1.65
TEV	10^{-1}	0.05	1.10
	10^{-2}	0.11	1.58
	10^{-3}	0.13	1.62
Healthy leaves		0.02	0.00
Soybean	10^{-1}	0.03	0.00
Cowpea	10^{-1}	0.01	0.00
Peanut	10^{-1}	0.00	0.00
Tobacco	10^{-1}	0.00	0.00
White lupine	10^{-1}	0.02	0.00

[a] Leaf tissue extracted at 1 g per 9 ml of antigen extraction buffer = 10^{-1} dilution.
[b] Crude antisera used at 1:1,000 dilution. Values (A_{410}) represent average of two replications.

sions were observed in the cytoplasm of white lupine, Little Marvel pea, sesame, and cowpea infected with the sesame isolate. Inclusions of WMV-2 in *N. benthamiana* were indistinguishable from inclusions induced by the sesame isolate (Fig. 3).

DISCUSSION

Potyviruses compose the largest plant virus group and cause serious diseases in crops throughout the world (9). The causal virus of sesame mosaic disease was identified as a potyvirus based on its flexuous rod-shaped particles, mechanical transmission, nonpersistent transmission by aphids, cytoplasmic inclusions, physical and chemical characteristics, and serological relationship with other potyviruses.

Biological properties, such as host range, cross-protection, vector transmissibility, and serology, and chemical properties, such as peptide mapping of virus coat proteins and nucleotide sequence homology of virus genomes, are used as criteria to distinguish the viruses within a group and the strains of a given virus. Potyviruses are known to infect sesame naturally and in the laboratory (2,10, 25,26). We tested the susceptibility of sesame to BlCMV, PMV, PSBMV, PStV, SMV, and WMV-2 by sap inoculation in the laboratory, and it was infected by all of these viruses. The comparison of host ranges of the sesame isolate with those of BlCMV, PGMV, PMV, PSBMV, PStV, and TEV suggests that the sesame isolate is different from these viruses even though it reacted with antisera to many of these viruses (Tables 2 and 3). Weak reactions between potyviruses often result if the antibodies are against core proteins in addition to terminal epitopes. We consider the sesame isolate to be distinct from the two viruses naturally infecting peanut, PMV and PStV, in the United States because it did not infect peanut but did infect cucurbits, whereas PMV and PStV did not infect cucurbits. Of the viruses tested by ELISA (Table 2), only the sesame isolate and WMV-2 infected squash and pumpkin, and immunodiffusion tests clearly distinguish these two viruses. Although differences in biological properties and serology clearly distinguish the sesame virus as a new potyvirus, we have not designated a new virus name. Instead we have documented some properties of this virus that naturally infects sesame in North America. Since seed transmission of the sesame isolate was not detected, the virus is possibly indigenous to the United States.

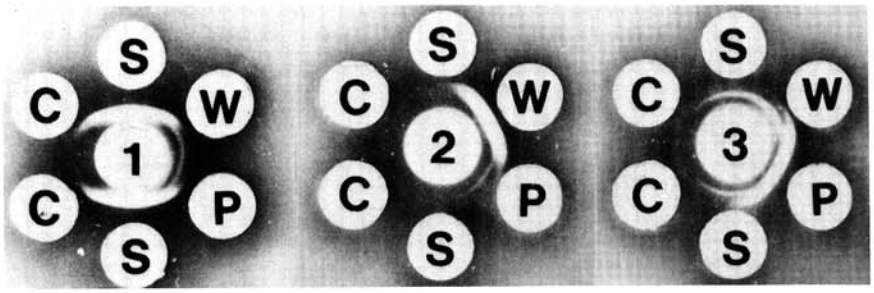

Fig. 2. Serological evidence that the potyvirus from sesame is different from, but related to, watermelon mosaic virus 2 and peanut stripe virus was obtained by conducting immunodiffusion tests in agar media containing sodium dodecyl sulfate (SDS). The outer wells of each seven-well pattern contain SDS-treated extracts from *Nicotiana benthamiana*; S = infected with the potyvirus from sesame, W = infected with watermelon mosaic virus 2, P = infected with peanut stripe virus, and C = noninoculated control plants. The center wells contain undiluted antiserum to 1 = sesame potyvirus, 2 = watermelon mosaic virus 2, and 3 = peanut stripe virus.

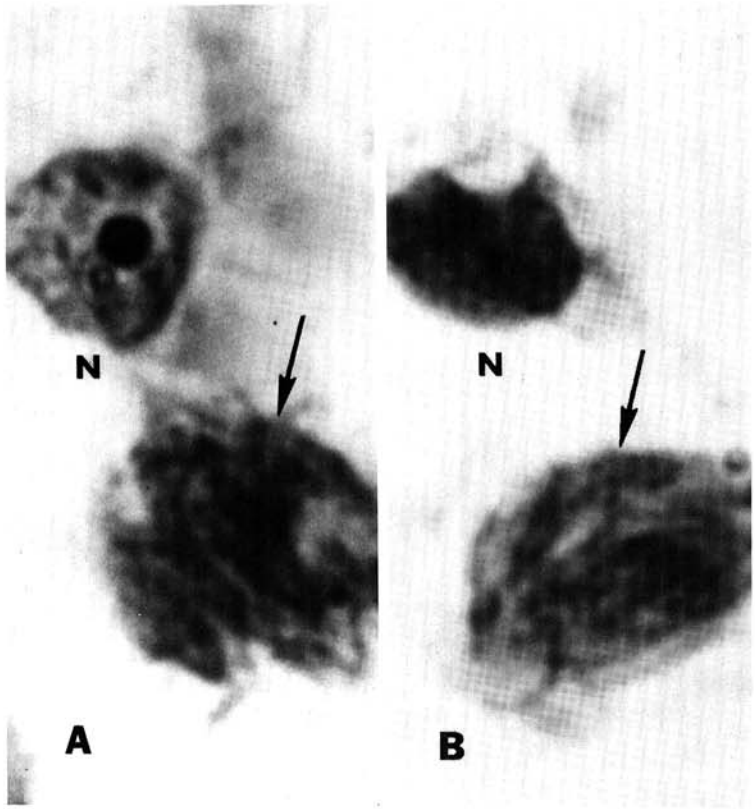

Fig. 3. Light micrographs of cytoplasmic cylindrical inclusions (arrows) induced by **(A)** the sesame isolate virus and **(B)** watermelon mosaic virus 2 (×4,203). N = nucleus.

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