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A new flower breaking tobamovirus of *Streptocarpus*

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Abstract

A virus was isolated from *Streptocarpus* plants that showed colour breaking of the flowers. Initial diagnostic tests indicated that this virus was a member of the Tobamovirus genus. The virus could be transmitted mechanically to several test plants. Its stability in plant sap was in line with that of other tobamoviruses, i.e. infectivity was lost after 10 min incubation at 90 °C and after dilution to 10^{-8}. In addition, the morphology of the virus was typical for tobamoviruses. The particles had a length of about 304 nm. On test plants, the virus from *Streptocarpus* could be distinguished from 7 well-defined tobamoviruses. *Nicotiana glutinosa* showed the most characteristic symptoms. In agar double-diffusion tests and/or double antibody sandwich enzyme-linked immunosorbent assays, no cross reactivity was observed in heterologous combinations with these 7 and 3 other tobamoviruses. Mechanical inoculation of the virus to virus-free *Streptocarpus* plants resulted in the appearance of flower breaking in about 50% of the plants. On the basis of these findings, it is concluded that the virus that causes flower breaking in *Streptocarpus* is a distinct member of the Tobamovirus genus, and the name *Streptocarpus* flower-break virus is proposed.

Introduction

In 1990 the virological section of the Plant Protection Service in the Netherlands received plants of *Streptocarpus* sp. (Family: Gesneriaceae) for diagnosis. The plants showed colour breaking of the flowers. This flower break could be observed in pink, purple as well as blue cultivars (Fig. 1). In most plants no leaf symptoms were observed, although occasionally chlorotic ring or line patterns occurred on one or two leaves (Fig. 2).

Inoculation of plant sap to herbaceous test plants and electron-microscopical examination, revealed the presence of a tobamovirus. Additional inoculation and immunodiffusion tests indicated that the virus from *Streptocarpus* was different from the tobamoviruses described so far, including

Fig. 1. Breaking of the pink colour on *Streptocarpus* flowers.

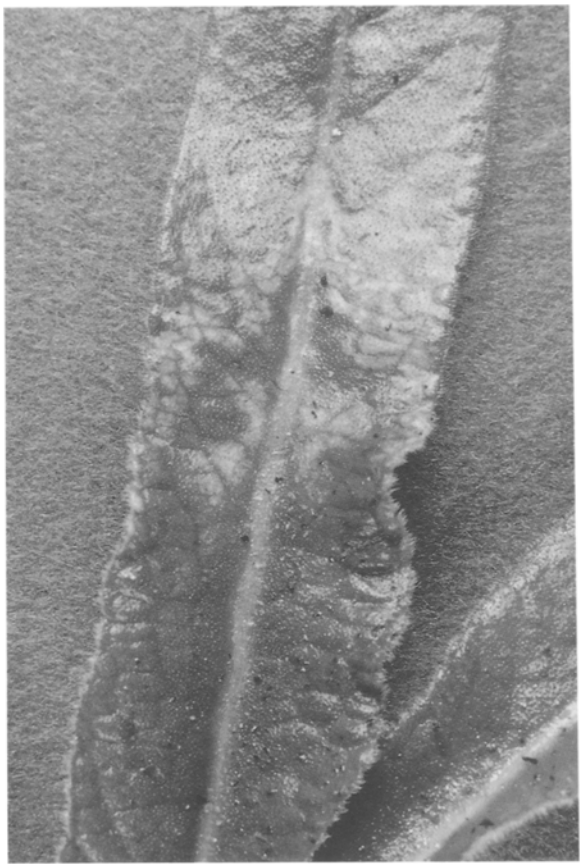

Fig. 2. Chlorotic line pattern on a leaf of *Streptocarpus*.

the two strains of tobacco mosaic virus (U1 and U2) that were reported for Gesneriaceae by Zettler and Nagel [1983]. These strains are now known as the type strain of tobacco mosaic virus [TMV; Zaitlin and Israel, 1975] and tobacco mild green mosaic virus [TMGMV; Wetter, 1989], respectively. In *Streptocarpus* samples only strain U2, i.e. TMGMV, was found.

In this paper the partial characterization is presented of a new tobamovirus for which the name *Streptocarpus* flower-break virus (SFBV) is proposed.

Materials and methods

Sources of viruses and antisera. SFBV was isolated from *Streptocarpus* plants that were obtained from a glasshouse in Ouderkerk aan de Amstel, the Netherlands. Purified preparations of TMGMV, isolates PV0112 and PV0124 [Wetter, 1989], and antiserum to PV0112 were gifts from G. Adam, Germany. Purified preparations of bell pepper mottle virus [BePMV, Wetter *et al.*, 1987], cucumber green mottle mosaic virus [CGMMV, Hollings *et al.*, 1975], pepper mild mottle virus [PMMV, Wetter and Conti, 1988], TMV strain U1 [Zaitlin and Israel, 1975], tomato mosaic virus strain dahlemense (ToMV-D) and strain Ohio 3 [ToMV-O3, Hollings and Huttinga, 1976], dried leaf material of *Chenopodium quinoa* infected with *Odontoglossum* ringspot virus [ORSV, Paul, 1975] and the homologous antisera were kindly provided by D.Z. Maat, IPO-DLO.

Virus propagation and purification. SFBV was isolated from *Streptocarpus* by sap inoculation to carborundum-dusted leaves of *Nicotiana benthamiana*. The inoculum was prepared by grinding *Streptocarpus* leaf material in inoculation buffer [0.02 M phosphate buffered-saline (PBS) containing 2% (w/v) polyvinylpyrrolidone (PVP; MW 10,000)]. The inoculated plants were grown in a greenhouse at 18–25 °C, with supplemental illumination for a daylength of at least 12 h.

The other tobamoviruses were propagated in the following hosts: *C. quinoa* (ORSV), *Cucumis sativus* 'Gele Tros' (CGMMV), *Lycopersicum esculentum* 'Ailsa Craigh' (ToMV-D and -O3), *N. benthamiana* (PMMV and TMGMV), *N. occidentalis*-P1 (BePMV), *N. tabacum* 'White Burley' (TMV).

For purification of SFBV, infected leaves of *N. benthamiana* were harvested 14 days after inoculation. The virus was purified according to the method described by Tóbiás *et al.* [1982b]. To estimate virus concentrations, the extinction coefficient at 260 nm for a solution containing 1 mg virus per ml was assumed to be 3.1.

Inoculation of Streptocarpus. A purified preparation (2 μg ml^{-1}) of SFBV was inoculated mechanically to 19 virus-free *Streptocarpus* plantlets. The plants were held in the greenhouse under conditions as described for virus propagation and were inspected for symptoms at regular intervals during one year. Three months after inoculation all plants were screened for the presence of virus in double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA).

Comparative study on test plants. Infected leaves from propagation hosts (stored at –20 °C) were used for inoculation. Each virus was inoculated to four plants of all the species given in Table 1. Plants were inspected for virus symptoms during the following three weeks. Then virus presence was indexed in DAS-ELISA by testing leaves with systemic symptoms or, when these were absent, by testing both the inoculated and youngest leaves.

Stability in sap. The thermal inactivation point of SFBV was determined by incubation of plant sap from infected *N. benthamiana* plants for 10 minutes at 80, 85, 90, 95 and 100 °C, respectively. The dilution end point was determined with decimal dilutions of similar plant sap (10^{-3}–10^{-9}) in distilled water. Indexing was by inoculation of four *N. glutinosa* plants.

Electron microscopy. Leaves from infected *N. benthamiana* were chopped in 2% potassium phosphotungstate, pH 6.5. This preparation was mounted on formvar carbon-coated grids and examined in a Philips CM 12 electron microscope. Particles were measured on enlarged electron micrographs and grouped into classes of 10 nm. The average length of SFBV particles was calculated by comparison with TMV particles estimated to measure 300 nm in average.

Antiserum production and serology. For production of antiserum to SFBV, three subcutaneous injections with 5 mg of virus emulsified in Freund's incomplete adjuvant were given to a rabbit at intervals of three weeks. Bleedings were started three weeks after the last injection, and were continued at intervals of three weeks. The second bleeding was immediately followed by a fourth subcutaneous injection.

Coating immunoglobulin (IgG) and alkaline-phosphatase conjugated IgG were prepared from the third bleeding according to Tóbiás *et al.* [1982a].

Agar double-diffusion tests were performed in 0.6% (w/v) purified Difco agar in 0.01 M PBS, containing 0.05% (w/v) sodium azide. IgG (1 mg ml^{-1}) and antigens (undiluted or 4-times diluted plant sap) were added to wells with a diameter of 3 mm at a distance of 5 mm. For CGMMV purified virus (16 mg ml^{-1}) was used. Results were read after incubation at room temperature for 24 and 48 h.

DAS-ELISA was performed according to Clark and Adams [1977] with minor modifications. Microtiter plates (M129A, Dynatech) were coated with IgG (1 μg ml^{-1}, except for TMGMV which was used at 17 μg ml^{-1}). Antigen preparations were diluted to 25 μg ml^{-1} for purified virus, or 0.1 g ml^{-1} for infected leaf material, in 0.02 M PBS containing 0.05% (v/v) Tween, 2% (w/v) PVP and 0.2% (w/v) ovalbumin. Conjugate concentration was 0.25 μg ml^{-1} for CGMMV, ORSV and SFBV, 0.5 μg ml^{-1} for BPeMV, PMMV, TMV, ToMV-D and ToMV-O3, and 6.8 μg ml^{-1} for TMGMV. Incubation with coating, antigen preparation, as well as conjugate was for 24 h at 4 °C. Hydrolysis of the substrate para-nitrophenyl phosphate (0.75 mg ml^{-1}) was measured with a Titertek Multiskan photometer at 405 nm, after 1, 2 and 4 h incubation at 30 °C.

Results

Virus propagation and purification. N. benthamiana was a suitable host for propagation and purification of SFBV. Virus yield was about 1 mg g^{-1} of fresh tissue.

Inoculation of Streptocarpus. From the 19 *Streptocarpus* plants that were inoculated with SFBV, 16 were found to be infected in DAS-ELISA. Unexpectedly, these did not show any flower breaking up to one year after inoculation. However, symptoms did occur when plants, grown from cuttings of one infected plant, were re-inoculated at the onset of flowering. These cuttings were taken 6 months after the first inoculation. About 3 weeks after re-inoculation flower breaking was observed in 8 of 15 plants, grown from these cuttings. Testing in DAS-ELISA four weeks later revealed that SFBV was present in all 15 plants.

TMV-inoculated and non-inoculated (control) plants gave consistently negative ELISA responses.

Table 1. Comparison of symptoms induced by the tobamovirus from *Streptocarpus* (SFBV) with those induced by other tobamovirus species in several test plants. The presence of virus was determined in DAS-ELISA

Test plant	Virus															
	BePMV[1]		CGMMV		ORSV		PMMV		SFBV		TMGMV		TMV		ToMV-D		ToMV-O3	
Capsicum annuum 'Lolo'	–*	S_{cv}[2]	(l)	–	l	–	–*	S_{cv}	l	–	–*	$S_{cv!}$	–*	S_{cv}	–*	S_{cv}	–*	S_{cv}
Chenopodium quinoa	L_{cn}	s	l	–	L_{cn}	–	L_{cn}	–	L_{cn}	–	L_{cn}	–	L_{cn}	–	L_{cn}	–	L_{cn}	–
Cucumis sativus 'Gele Tros'	–	–	–*	S_{lm}	–	–	–	–	L_c	–	L_c	–	L_c	–	L_c	–	L_c	–
Datura stramonium	L_n	–	l	–	–	–	L_n	–	L_n	–	L_n	–*	L_n	–	L_n	–	L_n	–
Lycopersicum esculentum 'Moneymaker'	–	–	–	–	–	–	–	–	l	–	–*	–*	–*	S_m	–*	S_m	–*	S_m
Nicotiana benthamiana	L_c	S_{cl}	l	s	–*	S_{lm}	l	S_l	–*	S_m	–*	$S_{ln!}$	–*	$S_{cln!}$	–*	$S_{ln!}$	–*	S_m
N. clevelandii	–*	.	(l)	.	l	s	–*	.	l	S_m	–*	S_m	–*	S_m	–*	S_m	–*	S_{cm}
N. glutinosa	L_n	–	(l)	–	L_n	–	L_n	–	L_{cn}	–	L_n	S_n	L_n	S_n	L_n	S_n	L_n	S_n
N. occidentalis–P1	l	S_{cln}	–	–	L_{cn}	–	L_n	S_{cln}	–*	S_m	–*	$S_{ln!}$	–*	$S_{cl!}$	–*	$S_{ln!}$	–*	$S_{ln!}$
N. rustica	L_{cn}	–	l	–	–	–	L_{cn}	–	L_c	–	L_{cn}	–*	–*	$S_{clv!}$	L_{cn}	S_{ln}	L_{cn}	S_{ln}
N. sylvestris	L_n	–	–	–	–	–	.	.	(l)	–	$L_{n!}$	–*	L_n	S_m	L_n	–	L_n	–
N. tabacum 'Samsun'	(l)	S_{lm}	l	–	l	–	l	–	l	–	–*	S_m	–*	S_m	l	S_c	–*	S_m
N. tabacum 'White Burley'	L_{cn}	–	–	–	–	–	L_{cn}	–	L_{cn}	–	L_{cn}	$S_{cn!}$	–*	S_m	L_{cn}	–	L_{cn}	$S_{cv!}$
Phaseolus vulgaris 'Dubbele Witte, zonder draad'	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Petunia hybrida 'Polo Pink'	L_n	–	l	–	–	–	L_n	S_{cl}	L_n[3]	–	L_n	S_l	–*	S_{cln}	L_n	–	L_{cn}	$S_{cln!}$

[1] BePMV = bell pepper mottle virus; CGMMV = cucumber green mottle mosaic virus; ORSV = *Odontoglossum* ringspot virus; PMMV = pepper mild mottle virus; TMGMV = tobacco mild green mosaic virus strain PV0112; TMV = tobacco mosaic virus; ToMV-D = tomato mosaic virus strain dahlemense, and ToMV-O3 = tomato mosaic virus strain Ohio 3.

[2] The first and second symbol denote the reaction of inoculated and non-inoculated leaves, respectively: L = local lesions; l = latent local infection; S = systemic symptoms; s = latent systemic infection; suffix c = chlorotic lesions; suffix l = leaf malformation; suffix m = mosaic or mottle; suffix n = necrotic symptoms; suffix v = vein clearing; suffix ! = decline; – = no infection; –* = no symptoms, but not tested for latent infection; ( ) = weak reaction in DAS-ELISA; . = not tested.

[3] Only 2 out of 4 plants were infected.

Symptomatology of SFBV and comparative study on test plants. Upon inoculation with SFBV, the following plant species showed only local reactions:

- *C. quinoa*: small chlorotic lesions, often with a necrotic centre, after 7 days;
- *C. sativus* 'Gele Tros': pin-point chlorotic lesions after 7 days;
- *Datura stramonium*: small necrotic lesions after 5–6 days;
- *N. glutinosa*: small to rather large chlorotic lesions (2 to 5 mm), sometimes with necrotic centres, after 5–6 days; lesions could grow or become more necrotic in the days that followed; characteristically, however, some lesions remained chlorotic (Fig. 3);
- *N. rustica*: small chlorotic lesions after 10 days;
- *N. tabacum* 'White Burley': chlorotic and necrotic lesions after 3 days;
- *Petunia hybrida* 'Polo Pink': occasionally very small necrotic lesions after 10 days.

Systemic symptoms were recorded for the following *Nicotiana* species:

- *N. benthamiana*: rugosity and leaf curling after 1 week; faint mosaic after 2 weeks;
- *N. clevelandii*: faint vein clearing after 15 days, becoming more pronounced during the following days; rugosity, leaf distortion and chlorosis of the youngest leaves;
- *N. occidentalis*-P1: small necrotic lesions mainly on the youngest leaves after 1 week, followed by leaf curling, chlorosis and severe stunting, within a few days.

No symptoms were observed in *Capsicum annuum* 'Lolo', *L. esculentum* 'Moneymaker', *N. sylvestris*, and *N. tabacum* 'Samsun'. These plants appeared to be only locally infected. *Phaseolus vulgaris* 'Dubbele Witte, zonder draad' was not infected at all.

Table 1 summarizes the results of the reaction of SFBV on several test plants in comparison with other tobamoviruses. It is clear that both the host range and symptom expression of SFBV are different from those of all the other viruses tested, the closest being ORSV. *N. glutinosa* is useful for discriminating SFBV from other tobamoviruses on

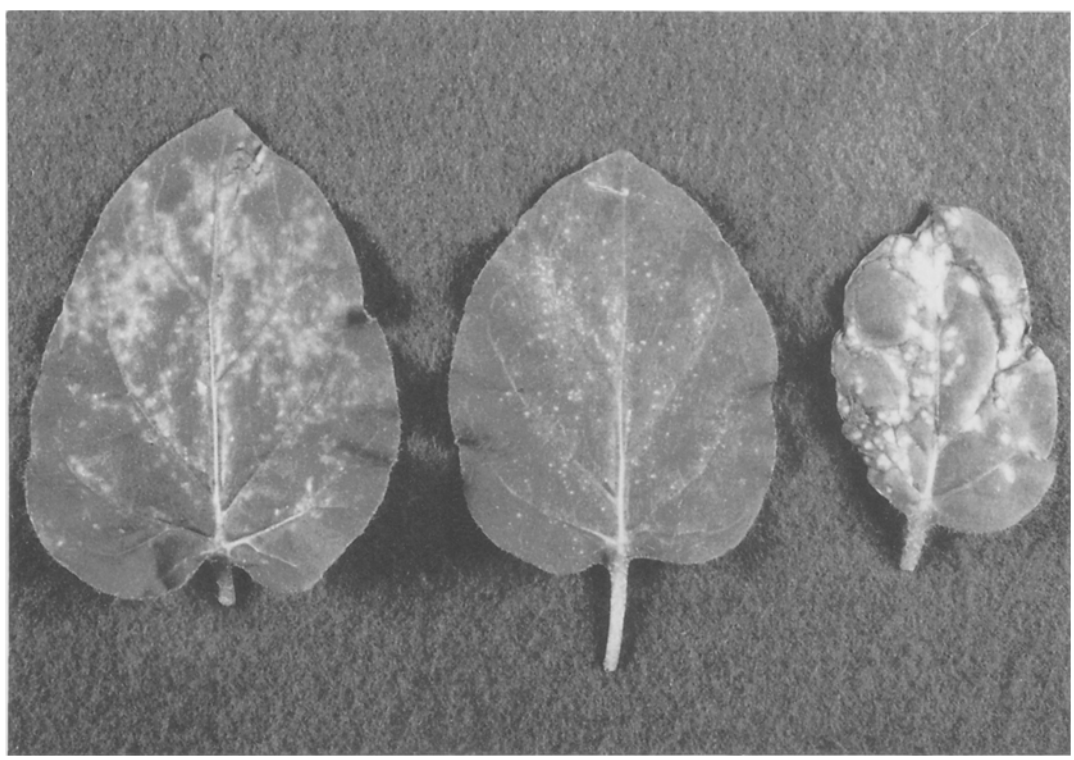

Fig. 3. Leaves of *Nicotiana glutinosa* showing local symptoms after mechanical inoculation of SFBV (left), ORSV (middle) and TMV (right), respectively.

the basis of symptomatology. However, for discrimination of SFBV from ORSV, it is advisable to include *N. tabacum* 'White Burley'.

Stability in sap. Thermal inactivation for SFBV in *N. benthamiana* occurred after 10 min at 90 °C. Dilution end-point was 10^{-8}.

Electron microscopy. Virus particles of SFBV were easily detected in crude sap preparations (Fig. 4). They appeared as rigid rods with an internal canal, which is typical for tobamoviruses. Their normal length was 304 nm, based on length measurements of 158 particles that occurred in the main peak. The particle width was about 18 nm.

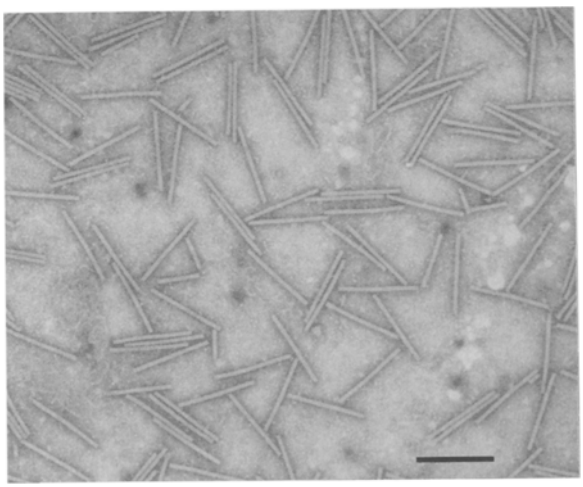

Fig. 4. Virus particles in leaf extracts of mechanically infected *Nicotiana benthamiana*, negatively stained with 2% potassium phosphotungstate, pH 6.5. Bar represents 300 nm.

Antiserum production and serology. After three injections, the homologous titre of antiserum was 256 in micro-precipitin test. Further injections increased the titre to 1024 for a short period. The antiserum used for the immunodiffusion tests and DAS-ELISA had a titre of 1024.

In the agar double-diffusion tests SFBV precipitated with its homologous antiserum in a double line. It did not react with antisera raised to BePMV, CGMMV, ORSV, PMMV, TMGMV, TMV, ToMV-D and ToMV-O3 (Fig. 5). No precipitation was obtained for SFBV antiserum with the heterologous viruses (results not shown).

In DAS-ELISA SFBV only reacted with its homologous antiserum, which did not react with any of the above mentioned tobamoviruses (Table 2).

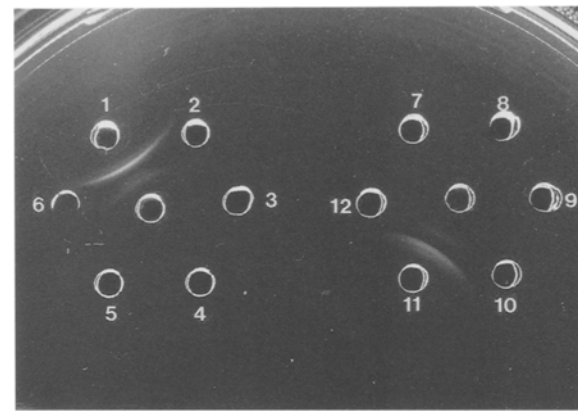

Fig. 5. Agar plate showing the results of double-diffusion tests for SFBV. Wells in the centres contain SFBV. Surrounding wells contain buffer (5 and 9) and antiserum to BePMV (2), CGMMV (10), ORSV (4), PMMV (3), TMGMV (12), TMV (8), ToMV-D (7), ToMV-O3 (6) and SFBV (1 and 11).

Discussion

Initial diagnostic tests indicated that the virus isolated from *Streptocarpus* plants that showed flower breaking, was a tobamovirus. This was confirmed by experiments that showed its transmissibility by contact, its stability in plant sap and the morphology of its particles [Gibbs, 1977]. Subsequent host range and serological studies revealed that this virus could be clearly distinguished from all other tobamoviruses examined. In addition, agar gel immunodiffusion tests performed by C. Wetter (personal communication) did not reveal any evidence that the virus from *Streptocarpus* was related to ribgrass mosaic virus (RMV), Sammons' opuntia virus and sunn-hemp mosaic virus (SHMV). Moreover, the virus from *Streptocarpus* clearly differs in host range and symptom expression from RMV [Oshima and Harrison, 1975; Wetter, 1986], SHMV [Kassanis and Varma, 1975], and also from frangipani mosaic virus [Varma and Gibbs, 1978] and tobamoviruses occurring in avocado [Alper *et al.*, 1978], *Passiflora edulis* [Fribourg *et al.*, 1987], rose [Hicks and Frost, 1984] and turnip [Lartey

Table 2. Comparison of the tobamovirus from *Streptocarpus* (SFBV) with other tobamovirus species on basis of its serological reactions in DAS-ELISA. Table shows the absorbance values at 405 nm after 4 hours of substrate incubation

Antigens	Antisera								
	BePMV[1]	CGMMV	ORSV	PMMV	SFBV	TMGMV-PV0112	TMV	ToMV-D	ToMV-O3
BePMV	> 2.00	0.02	0.00	0.25	0.15	0.38	0.04	0.44	0.92
CGMMV	0.02	> 2.00	0.00	–0.02	0.03	0.08	0.01	0.00	0.02
ORSV	0.21[3]	–0.04[3]	> 2.00[4]	–0.04[3]	0.04[2]	0.77[4]	0.03[4]	0.07[2]	0.18[2]
PMMV	0.47	0.03	0.00	> 2.00	0.03	0.58	0.01	0.03	0.20
SFBV	0.01	–0.07	0.00	–0.05	> 2.00	0.18	0.01	0.02	0.05
TMGMV-PV0124	0.08	–0.03	0.02	0.01	0.04	> 2.00	0.03	0.00	0.00
TMGMV-PV0112	0.07	–0.02	0.00	0.09	–0.01	> 2.00	0.00	1.56	–0.04
TMV	0.06	0.01	–0.01	–0.05	0.03	0.90	> 2.00	> 2.00	0.58
ToMV-D	0.09	–0.02	0.00	0.02	0.04	0.84	0.01	> 2.00	> 2.00
ToMV-O3	0.09	0.02	0.00	0.03	0.03	0.47	0.03	0.30	> 2.00

[1] BePMV = bell pepper mottle virus; CGMMV = cucumber green mottle mosaic virus; ORSV = *Odontoglossum* ringspot virus; PMMV = pepper mild mottle virus; TMGMV-PV0112 = tobacco mild green mosaic virus strain PV0112/0124; TMV = tobacco mosaic virus; ToMV-D = tomato mosaic virus strain dahlemense, and ToMV-O3 = tomato mosaic virus strain Ohio 3.

[2] From dried leaf material (50× diluted; *Nicotiana clevelandii*).

[3] From frozen leaf material (12.5× diluted; *N. tabacum* 'Samsun').

[4] From frozen leaf material (10× diluted; *Chenopodium quinoa*).

et al., 1993]. Furthermore, amino acid analysis indicated that the *Streptocarpus* virus is different from any of the tobamovirus species analysed so far (Van Regenmortel and Saunal, personal communication).

The virus from *Streptocarpus* could be transmitted mechanically to virus-free *Streptocarpus* plants. Unexpectedly, at first instance no flower breaking appeared in the infected plants. However, in the plants grown from cuttings from one of these infected plants, re-inoculation at the onset of flowering resulted in the appearance of flower breaking symptoms in about half of the plants. Since the plants that showed symptoms were located nearest to the outer glass-wall of the greenhouse, it was assumed that light conditions may play a role in the expression of symptoms. Besides, the fact that this particular tobamovirus could be detected in all incoming *Streptocarpus* plants that showed flower breaking, provides additional evidence that it indeed causes these symptoms.

On the basis of the findings presented in this paper, it is concluded that the virus that causes flower breaking in *Streptocarpus* is a distinct species of the Tobamovirus genus, for which the name *Streptocarpus* flower-break tobamovirus is proposed.

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