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Tobamoviruses of pepper, eggplant and tobacco: comparative host reactions and serological relationships

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Abstract

Using test plants and serology six tobamoviruses of pepper (FO, Ob, P8, P11, P14 and SL) and one of eggplant (A1) were compared with common tobacco mosaic virus (TMV-WU1). WU1, A1 and FO were closely similar in their reactions in *Capsicum* spp. as were P14 and SL. Ob, P11 and P8 were also similar in this respect except in *C. frutescens* 'Tabasco' in which P8 differed from Ob and P11.

Using micro-precipitation tests the virus strains could be roughly divided into three serological groups: Group I consisted of WU1, group II of A1, FO, P8, P14 and SL, and group III of P11 and Ob. With ELISA group II was further divisible into two subgroups, including A1 and FO, and P8, P14 and SL.

It was concluded that similarities of strains in their reactions in *Capsicum* spp., were not necessarily confirmed by their serological relationships.

Additional keywords: tobacco mosaic virus, ELISA, resistance breeding.

Introduction

In the one hundred years of research on tobamoviruses many strains have been isolated from numerous plant species in many parts of the world. In a recent review, Van Regenmortel (1981) classified the strains as comprising: tobacco mosaic virus, strain vulgare (henceforth referred to as 'common' TMV), tomato mosaic virus strains, *Plantago* strains, legume strains, cucurbit strains, orchid strains, strain U2, and other strains. Among the latter was the 'pepper unusual strain', isolated in Argentina by Feldman and Oremianer (1972).

Another pepper isolate occurring in the USA was described as the 'Samsun latent strain' by McKinney (1952). This strain was later investigated by Greenleaf et al. (1964). In Hungary, Burgyán et al. (1978) investigated two pepper isolates. One was found to be identical with 'common' TMV, but the other differed serologically from both tobacco and tomato mosaic virus strains. Another Hungarian pepper isolate,

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used in breeding work, was briefly described by Csilléry and Ruskó (1980). In the Netherlands, Rast (1979) isolated two pathogenically distinct strains from pepper tentatively identified as the 'Samsun latent strain' and the 'pepper unusual strain' of TMV. Maat (1981) found that these strains were serologically related, but not identical. A third pepper strain was reported by Boukema et al. (1980) to overcome the resistance of *Capsicum chinense* accessions to the two other Dutch strains.

In view of the economic losses in pepper caused by tobamoviruses and the resulting efforts to breed for TMV resistance in this crop (Villalón, 1981), we have compared six pepper strains with an isolate of 'common' TMV and an isolate from eggplant *(Solanum melongena),* also found to infect pepper. The main object of these investigations was to determine whether a differentiation according to their host reactions corresponded with a grouping on the basis of their serological properties.

Materials and methods

Virus strains. The strains tested (Table 1) were maintained in the following systemic hosts: WU1 in *Nicotiana tabacum* 'White Burley', A1 in *Solanum melongena* 'Dobrix', FO in *Capsicum annuum* 'Westlandia', Ob in *N. tabacum* 'Xanthi-nc', P11 in *C. annuum* 'Tisana', P8 in *C. frutescens* 'Tabasco', P14 and SL in *C. chinense* 'Miscucho'. For virus purification the strains were propagated in *N. clevelandii* except for strain Ob, which was purified from *N. tabacum* 'Xanthi-nc' as well as from *N. clevelandii.*

The test plants were raised in the glasshouse at 18° – 23° C with additional light in winter to provide a daylength of 12 h. After mechanical inoculation the plants were grown under natural light conditions (Rast, 1979).

Table 1. Tobamovirus strains tested.

Strain or isolate	Original host	Author(s)
WU1	tobacco	Van Loon and Van Kammen, 1970, and personal communication
A1	eggplant	A.Th.B. Rast, 1980 (unpublished)
FO[1]	pepper	Feldman and Oremianer, 1972
Ob	pepper	Csilléry and Ruskó, 1980
P11, P8	pepper	Rast, 1979
P14	pepper	Boukema et al., 1980
SL	pepper	Mckinney, 1952; Greenleaf et al., 1964

[1] Abbreviation introduced by the present authors to indicate the 'unusual pepper strain' of TMV.

Tabel 1. Getoetste tobamovirusstammen.

Virus purification. A1, FO, Ob, P14 and SL were purified by a modification of the method described by Gooding and Hebert (1967). Chilled leaf material was homogenized in McIlvaine's phosphate-citric acid buffer (PCA buffer; 0.18 M; pH 7) to

which 0.1% sodium thioglycolate (W/V) was added. The homogenate was thoroughly mixed with n-butanol (8% by volume), strained through cheesecloth and centrifuged for 10 min at 10 000 *g*. The supernatant was kept at 4° C overnight and centrifuged again for 10 min at 10 000 *g*. To the supernatant thus obtained, polyethylene glycol 6000 (peg) was added, 4 g of peg per 100 ml of liquid. After stirring for 60 min at room temperature and centrifugation for 10 min at 10 000 *g*, the sediment obtained was resuspended in PCA buffer. The suspension was centrifuged at 10 000 *g*. The supernatant was kept and the sediment again was resuspended in PCA buffer, the suspension being centrifuged for 10 min at 10 000 *g*. The two supernatants were combined and 2% Triton X-100 (V/V) was added before differential centrifugation (1 h at 90 300 *g*; 10 min at 10 000 *g*). This was then followed by two successive sucrose-gradient centrifugations (10-40% sucrose in PCA buffer; 2 h at 103 800 *g* in the Beckman SW 27 rotor). After each sucrose-gradient centrifugation, virus fractions were diluted 1 : 1 with PCA buffer and concentrated (1 h at 90 300 *g*). All *g*-values given are at R_{max}. Purified preparations were stored at $-18°$ C.

A purified preparation of WU1 was obtained from Dr L.C. van Loon, Department of Plant Physiology, Agricultural University, Wageningen. Purified preparations of P8 and P11 were available from earlier experiments (Maat, 1981) and prepared in various ways.

Antiserum preparation. Antisera to each of the WU1, A1, FO, Ob and SL strains were prepared by injecting one rabbit with two sets of injections, each set consisting of one intravenous and one intramuscular injection. The two sets were given with a two weeks' interval. Intravenous injections contained 2.5 mg of purified virus. For intramuscular injections, the same amount of virus was emulsified with Freund's incomplete adjuvant. Blood samples were taken every second or third week, starting two weeks after the second set of injections.

Antisera to P8 and P11 were from earlier experiments (Maat, 1981).

Serology. Antiserum titers were determined with the micro-precipitation test under paraffin oil (Van Slogteren, 1955). Twofold antiserum and fourfold antigen dilutions were made in 0.1 M tris-(hydroxymethyl)aminomethane buffer adjusted to pH 8 with 0.1 M citric acid and containing 0.05% sodium azide. Results were read after 24 h at room temperature.

The method described by Tóbiás et al. (1982) was used to prepare γ-globulin fractions and enzyme conjugates from antisera to WU1, A1, FO, Ob and SL. Such preparations from antisera to P8 and P11 were from earlier experiments (D.Z. Maat, unpublished). The γ-globulin fractions of the latter two were prepared in the same manner, but enzyme conjugates were prepared as described by Clark and Adams (1977).

Enzyme-linked immunosorbent assays (ELISA) were performed as described by Tóbiás et al. (1982), but enzyme conjugates were used 1000 times diluted (antisera to WU1, A1, FO and SL), or 250 times diluted (antisera to Ob, P8 and P11). Dilution series of purified antigens were made in phosphate-buffered saline (PBS; pH 7.4), containing 2% polyvinyl pyrrolidone 25 000, 0.05% Tween 20 and 0.05% sodium azide. Results were read after 1, 3 and 6 h substrate incubation at room temperature.

To prepare γ-globulins, antiserum samples used were from the first (Ob), second (A1) or third (WU1, FO and SL) bleedings. Those of P8 and P11 were from mixed antiserum samples (bleedings).

Table 2. Results of host plant tests, performed to compare tobamoviruses from tobacco (WU1), eggplant (A1), and pepper (FO, Ob, P8, P11, P14 and SL). Symbols used for description of symptoms on inoculated leaves/symptoms from systemic infection: a = abscission; c = chlorosis; d = deformation; L = local lesion reaction; m = mosaic or mottling; n = necrosis; n! = lethal necrosis; r = local ringspots; S = systemic reaction; s = latent infection, virus detected on bioassay on *N. glutinosa;* − = no symptoms, presence or absence of virus not verified by bioassay; −* = no symptoms, no virus detectable on bioassay on *N. glutinosa;* ( ) = inconsistently.

Host	Resistance genes	WU1	A1	FO	Ob	P11	P8	P14	SL
Capsicum annuum									
'Westlandia'	L^0 (L^+)	−/Sn!	−/Sn!	−/Snam	−/Sn!	−/Sm	−/Sm	−/Sm	−/Sm
'Early Calwonder'	L^0 (L^+)	−/Sm	−/Sm	−/Sm	−/Sm	−/Sm	−/Sm	−/Sm	−/Sm
'Javitott Cecei'	L^0 (L^+)	−/Sn	−/Sn	−/Sn	−/Snam	−/Sm	−/Smn	−/Sm	−/Sm
'Verbeterde Glas'	L^1 (L^i)	Lna/−	Lna/−	Lna/−	−/Sn!	−/Sm	−/Sm	−/Sm	−/Sm
'Ru-72-292'	L^1 (L^i)	Lna/−	Lna/−	Lna/−	Ln/Sn!	−/Sm	−/Snam	−/Snam	−/Smn
'D. Cecei'	L^1 (L^i)	Lna/−	Lna/−	Lna/−	−/Sn!	−/Sm	−/Smn	−/Smn	−/Sm
'Fehérözön'	L^1 (L^i)	Lna/−	Lna/−	Lna/−	−/Sn!	−/Sm	−/Sm	−/Sm	−/Sm
Capsicum chinense									
'D7'	L^1 (L^i)	Lna/−	Lna/−	Lna/−	−/Sm	−/Sm	−/Sm	−/Sm	−/Sm
'Mishme'	L^1 (L^i)	Lna/−	Lna/−	Lna/−	−/Sm	−/Sm	−/Sm	−/Sm	−/Sm
Capsicum frutescens									
'Tabasco'	L^2 (L)	Lna/−	Lna/−	Lna/−	Lna/Sn[1]	Lna/−	−/Sm	−/Sm	−/Sm
Capsicum chinense									
'D8'	L^3 (−)	Lna/−	Lna/−	Lna/−	Lna/−	Lna/−	Lna/−	−/Sm	−/Sm
'Miscucho'	L^3 (−)	Lna/−	Lna/−	Lna/−	Lna/−	Lna/−	Lna/−	−/Sm	−/Sm
'P.I. 159236'	L^3 (−)	Lna/−	Lna/−	Lna/−	Lna/−	Lna/−	Lna/−	−/Sm	−/Sm
Chenopodium amaranticolor		Lna/−*	Lna/Smd	Lna/Smd	Lna/−*	Lna/−*	Lcn/−*	Lcn/−*	Lc/−*
Chenopodium quinoa		Lna/−*	Lna/Sm	Lna/Sm	Lna/−*	Lna/−*	Lna/−*	Lc/−*	Lc/−*
Lycopersicon esculentum									
'Moneydor +/+'		−/Sm	−/(s)	−/−*	−/Sm	−/−*	−/−*	−/−*	−/−*
'Craigella +/+'		−/Sm	−/−*	−/−*	−/Sm	−/−*	−/−*	−/−*	−/−*
'Craigella Tm-1/+'		−/Sm	−/−*	−/−*	−/Sm	−/−*	−/−*	−/−*	−/−*
Nicotiana rustica		Lcn/Sn!	Lcn/Scn	Ln/Sn	−/Smdn	Ln/−	Ln/−[2]	Ln/−[2]	Ln/−[2]
Nicotiana sylvestris		−/Smd	Ln/−	Ln/−	Ln/−	Ln/−	Ln/−	Ln/−	Ln/−

Nicotiana tabacum								
'Samsun'	−/Smd	−/Sm	−/s	−/Smd	−/−*	−/−*	−/s	−/s
'Xanthi-nc'	Ln/−	Ln/−	Ln/−	Ln/Snm	Ln/−	Ln/−[2]	Ln/−[2]	Ln/−[2]
Petunia hybrida	Lcn/Smd	Ln/−	Ln/−	Ln/−	Ln/−	Ln/−	Ln/−[3]	Ln/−[3]
Petunia nyctagyniflora	Lcn/Smd	Ln/−*	Ln/−*	−/Smd	−/Sm	−/Sm	−/Sm	−/Sm
Plantago major	−/−*	−/Sm	−/Sm[4]	Lr/−*	−/−*	−/−*	−/−*	−/−*
Solanum giganteum	Lna/−	−/Sm	−/Sm	−/Sm	−/s	−/s	−/s	−/s
Solanum melongena								
'Black Beauty'	Ln/Sn![5]	Ln/Sn![5]	Ln/(s)[6]	Ln/−*	(Ln)/−*	(Ln)/(s)	(Lc)/−*	−/(s)
'Dobrix'	Ln/Sm	−/Smn	−/(s)	Ln/−*	(Ln)/−*	(Ln)/−*	−/−*	(Ln)/−*
'Claresse'	−/Sm	−/Sm	−/(s)	Ln/s	−/−*	−/−*	−/−*	−/s
Solanum pseudocapsicum	Lna/−*	Lna/−*	Lna/−*	Lna/−*	−/Sm	−/Sm	Ln/−*[2]	Ln/−*[2]

[1] Only one out of eight plants reacted with a delayed systemic top necrosis.
[2] Small local lesions.
[3] Small whitish local lesions.
[4] One out of three plants gave local ringspots but was not systemically infected.
[5] Local lesions were not of the hypersensitive type.
[6] One out of six plants reacted with some systemic necrosis.

Tabel 2. Resultaten van toetsplantproeven, uitgevoerd ter vergelijking van tobamovirussen uit tabak (WU1), aubergine (A1) en peper (FO, Ob, P11, P8, P14 en SL).

Results

Host reactions. The reactions of 30/46 different test plants used are summarized in Table 2. The following test plants were omitted: *Lycopersicon esculentum* 'Craigella Tm-2nv/+', 'Craigella Tm-2^2/+', 'Craigella Tm-1/+.Tm-2nv/+' and 'Pérou-2', *Ocimum basilicum, Phaseolus vulgaris* 'Verschoor' and *Vigna unguiculata* subsp. *sesquipedalis* because they were not infected by any of the strains tested; *Datura stramonium, Gomphrena globosa, N. clevelandii* and *N. glutinosa* because they did not differentiate between strains; *Lycopersicon esculentum* 'CStMW-18', *N. megalosiphon, N. tabacum* 'White Burley' ('necrotic' line or 'Dutch A') and *Phaseolus vulgaris* 'Pinto' because they did not differ in reaction from other test plants included in Table 2; *N. glauca* because it was considered unsuitable as a test plant in this investigation.

Of the *Capsicum* hosts WU1 systemically infected only the generally susceptible *C. annuum* 'Westlandia', 'Javitott Cecei' and 'Early Calwonder'. The reactions of WU1 differed from those of all other strains in *N. sylvestris* and *Petunia hybrida* which developed systemic symptoms with WU1, whereas with the other strains only local lesions were observed. Another difference was observed in *S. giganteum* in which WU1 caused local lesions whereas all other strains caused systemic infection. Similarities were found between WU1 and the other strains with A1 in *S. melongena* and with Ob in *L. esculentum*.

A1 and FO were similar to WU1 in systemically infecting only the generally susceptible *Capsicum* hosts. They differed from the other strains by causing systemic symptoms in *Chenopodium amaranticolor, C. quinoa* and *Plantago major*. It should be noted that with FO, the systemic symptoms in these hosts (and in *N. rustica*) only developed when *C. annuum* 'Westlandia' was used as the source of inoculum and they were not observed using inoculum from *C. annuum* 'Early Calwonder'. A1 and FO caused local necrotic lesions in *P. nyctagyniflora* with some necrosis extending along main veins of uninoculated leaves, whereas all other strains caused systemic infection. A1 and FO gave distinguishable reactions in *S. melongena*. In the symptoms of this host A1 appeared similar to WU1. However, A1 killed plants of *S. melongena* 'Black Beauty' more rapidly and produced a more distinct mosaic than WU1 in *S. melongena* 'Dobrix'. Both A1 and WU1 only caused a very mild mottle in *S. melongena* 'Claresse'.

Compared with WU1, A1 and FO, Ob and P11 also caused systemic infection in *C. annuum* 'Verbeterde Glas', 'Ru-72-292', 'D. Cecei' and 'Fehérözön' and in *C. chinense* 'D7' and 'Mishme'. Between Ob and P11 there was a marked difference in the severity of symptoms in *C. annuum*. Similarities in host ranges of Ob and P11 were limited to the *Capsicum* hosts. The reactions caused by these strains in other test plants, notably *L. esculentum, N. rustica, N. tabacum* 'Samsun' and 'Xanthi-nc', *P. major* and *S. pseudocapsicum,* varied. Ob was distinct from P11 and all other strains by causing systemic symptoms in 'Xanthi-nc' and local ringspots in *P. major*.

In the *Capsicum* hosts, P8 differed from the other strains by causing mosaic symptoms in *C. frutescens* 'Tabasco' and it also differed from P14 and SL by causing local lesions in *C. chinense* 'D8', 'Miscucho' and 'P.I. 159236'. P8 was similar to P11, but differed from all other strains in failing to infect *N. tabacum* 'Samsun' and in systemically infecting *S. pseudocapsicum*. It should be noted that with P14 and SL, the latent

infection of 'Samsun' and the minute local lesions in *S. pseudocapsicum* resulted only when these strains had been first sub-cultured in *N. clevelandii.* P8, P14 and SL produced local lesions in *N. rustica* and *N. tabacum* 'Xanthi-nc' but they were consistently smaller than those caused by the other strains. This also applied to the whitish lesions of P14 and SL in *P. hybrida.*

Serology. The results of three micro-precipitation tests performed to compare the pepper strains, the eggplant isolate and the tobacco isolate are summarized in Table 3. Antisera to WU1, A1, FO, Ob and SL in the different experiments were from different bleedings. Antisera to P8 and P11 were the same in all experiments and therefore with these antisera the average titers of the three experiments are given. P14 was included in only one, and Ob in two experiments. From the results presented in Table 3, for each antiserum-antigen combination the serological differentiation index (SDI) was calculated. From these SDIs the average value of each combination and of its reverse were determined. These average SDIs are presented in Table 4. They show that the isolates can be roughly divided into three groups. WU1 is in group I. Group II consists of A1, FO, P8, P14 and SL. Average SDIs within this group are from

Table 3. Antiserum titers obtained in micro-precipitation tests to compare tobamoviruses from tobacco (WU1), eggplant (A1), and pepper (FO, P14, SL, P8, P11 and Ob).

Antisera	Exp.	Antigens							
		WU1	A1	FO	P14	SL	P8	P11	Ob
WU1	1	512	16	16		<4	<4	4	
	2	512	16	16		4	4	4	4
	3	1024	16	16	16	16	16	16	16
A1	1	64	1024	1024		512	128	16	
	2	32	1024	1024		256	256	32	32
	3	64	4096	2048	2048	1024	512	64	128
FO	1	64	1024	512		256	256	64	
	2	128	1024	2048		1024	256	128	64
	3	128	4096	2048	1024	1024	512	256	256
SL	1	64	128	128		512	128	64	
	2	64	128	256		512	256	64	64
	3	64	256	512	1024	1024	512	16	64
P8	1-3	128	1024	1024	1024	2048	1024	128	128
P11	1-3	16	64	64	128	128	64	1024	1024
Ob	2	16	16	32		16	4	128	256
	3	4	16	16	4	16	4	128	256

Tabel 3. Antiserumtiters in de micro-precipitatietoets verkregen bij vergelijking van tobamovirussen uit tabak (WU1), aubergine (A1), en peper (FO, P14, SL, P8, P11 en Ob).

Table 4. Average serological differentiation indices (SDIs) among tobamoviruses from tobacco (WU1), eggplant (A1) and pepper (FO, P14, SL, P8, P11, and Ob).

Antigens	Antisera						
	WU1	A1	FO	SL	P8	P11	Ob
WU1	–						
A1	5.16	–					
FO	4.00	0.00	–				
P14	6.00	1.00	1.00	0.00	0.00	3.00	6.00
SL	>5.00	1.83	1.16	–			
P8	>4.83	1.33	1.00	0.16	–		
P11	6.33	4.83	3.66	3.50	3.50	–	
Ob	5.75	4.50	3.75	3.66	4.50	0.50	–

Tabel 4. Gemiddelde serologische differentiatie indexen (SDI's) tussen tobamovirussen uit tabak (WU1), aubergine (A1) en peper (FO, P14, SL, P8, P11 en Ob).

0.00 – 1.83, while those in relation to the strains of the other groups are ⩾3.00. P11 and Ob are closely related (SDI 0.50) and belong to group III. The SDIs of this group in relation to those of the other groups are also ⩾3.00. All isolates are distantly related to WU1 (Table 3).

The results of ELISA experiments, using 5 μg of purified antigens per ml and read

Table 5. Extinction values in ELISA, obtained when comparing tobamoviruses from tobacco (WU1), eggplant (A1), and pepper (FO, P14, SL, P8, P11, and Ob).

Antigens[3]	Antisera						
	WU1[1]	A1[1]	FO[1]	SL[1]	P8[2]	P11[2]	Ob[2]
WU1	>1.20[4]	0.00	0.00	0.01	0.00	0.00	0.00
A1	0.01	>1.82	>2.00	0.16	0.23	0.00	0.00
FO	0.01	>1.62	>2.00	0.20	0.27	0.00	0.03
P14	0.01	0.08	0.31	1.31	1.18	0.00	0.00
SL	0.02	0.06	0.36	1.48	1.70	0.00	0.02
P8	0.01	0.03	0.48	1.67	>2.00	0.00	0.02
P11	0.01	0.02	0.01	0.04	0.03	>2.00	0.10
Ob	0.01	0.01	0.00	0.01	0.00	1.75	0.53

[1] Average of two experiments, two wells per experiment.
[2] Average of two wells in one experiment.
[3] Purified; concentration 5 μg ml^{-1}.
[4] After 6 h of substrate incubation.

Tabel 5. Extinctiewaarden in ELISA, verkregen bij vergelijking van tobamovirussen uit tabak (WU1), aubergine (A1) en peper (FO, P14, SL, P8, P11 en Ob).

after 6 h of substrate incubation, are presented in Table 5. They confirm the results obtained with the micro-precipitation tests. Using purified antigens at a fixed concentration, Group II could be subdivided into two groups. A1 and FO belong to one subgroup, and P8, P14 and SL to the other. When crude extracts from infected pepper plants were used in ELISA experiments, a clear division into (sub)groups was not possible, probably due to varying virus concentrations in pepper.

Discussion

By using various test plants in addition to *Capsicum* species, it was possible to differentiate the pepper strains studied from other tobamoviruses. Most of the pepper strains did not infect tomato, which confirmed the previous results of Feldman and Oremianer (1972), Rast (1979) and Greenleaf et al. (1964). Ob was justly given the prefix ToMV to denote tomato mosaic virus (Csilléry and Ruskó, 1980) and, in our opinion, it might be classified as tomato strain 1 (Pelham, 1972).

Eggplant was a poor multiplication host for most pepper strains. Of the two *Petunia* spp. tested, one became locally infected; the other became systemically infected by most of the pepper strains. By comparison, tomato and tobacco mosaic virus strains would cause local lesions and mosaic symptoms in both species respectively (Rast, 1975). FO was the only pepper strain which did not systemically infect *P. nyctagyniflora*.

The pepper strain FO closely resembled A1 in host range and symptom expression. It should be noted in particular, however, that in *Chenopodium* spp., *N. rustica* and *P. major* the reactions were different from those reported by Feldman and Oremianer (1972). This may be explained by differences in the source of inoculum used and possibly also by differences in sensitivity among test plants of the corresponding species (Van der Want et al., 1975). Because FO caused systemic infections only in three generally susceptible *Capsicum* hosts (Table 2), it was the least pathogenic of all pepper strains used. It is therefore not identical to P11 as previously suggested by Rast (1977).

Although varying greatly in host range and symptom expression, Ob and P11 were similar in pathogenicity towards the *Capsicum* hosts. In contrast to P11, which is characterized by green mosaic symptoms throughout the year, Ob caused considerably more necrosis in the *C. annuum* cultivars carrying the L^1 (L^i) gene for resistance under the experimental winter conditions, but normally Ob produces conspicuous, yellow mosaic symptoms (Csilléry and Ruskó, 1980). Ob was also reported to overcome the L^2 (L) gene for resistance in *C. frutescens* 'Tabasco'. In our experiments, using inoculum from *N. tabacum* 'Xanthi-nc', only one out of eight 'Tabasco' plants reacted with systemic necrosis after inoculation with Ob (Table 2). However, when using inoculum from *C. chinense* 'Mishme', Ob did cause a systemic mosaic in 'Tabasco', thus confirming the results of Csilléry and Ruskó (1980). Obviously the pathogenicity of this and of other strains under experimental conditions depends on the host in which they are maintained.

In the *C. chinense* accessions carrying the L^3 gene for resistance (Boukema et al., 1980) P8 was confirmed to be less pathogenic than P14 and, consequently, also appeared less pathogenic than SL. The latter result did not support the assumption that P8 would be closely related, if not identical to SL (Rast, 1977). However, correspondence between L. van den Berkmortel (Naaldwijk, the Netherlands) and R. Subrama-

nya (Gainesville, Florida, USA) in 1978 suggested possible differences in pathogenicity among isolates of SL in the USA. Three selections of the *C. chinense* accession P.I. 152225, resistant to P8, were also resistant to the isolate of SL used in Florida. The same accession was found to be susceptible to P14 (Boukema et al., 1980) which appeared similar to the isolate SL from Louisiana used in this work. It is therefore logical to assume that P8 and P14 are each identical to a different isolate of SL in the USA.

According to Van Regenmortel (1981) serology provides one of the most specific and rapid means of identifying individual TMV strains. Among the serological techniques available, the intragel cross-absorption test is recommended to differentiate between the major groups of tobamoviruses. Van Regenmortel and Burckard (1980) were also able to differentiate between serologically closely related strains, using the double-antibody sandwich method of ELISA. Using micro-precipitation tests, we could separate the strains investigated into three major groups. A further division of group II into two subgroups became evident from the ELISA tests.

A comparison of the grouping of the strains investigated on the basis of their reactions in *Capsicum* spp. and on the basis of their serological relationships is given in Table 6. The results of our experiments show that tobamoviruses giving similar reactions in *Capsicum* spp., can differ considerably in their serological properties. In addition, isolates that are different in their reactions in *Capsicum* spp. may be serologically very closely related.

As a practical consequence for TMV resistance breeding in pepper it may be concluded that for the identification of pepper strains of TMV, breeders should rely on differential *Capsicum* hosts rather than on serological methods.

Table 6. Grouping of tobamoviruses from tobacco (WU1), eggplant (A1), and pepper (FO, P14, SL, P8, P11, and Ob) on the basis of their reactions in *Capsicum* spp. and on the basis of their serological relationships.

Grouping on the basis of	Group	Strains
Reactions in *Capsicum* spp.	1	WU1, A1, FO
	2	P14, SL
	3	P8, P11, Ob
Serological relationships	1	WU1
	2 a	A1, FO
	b	P14, SL, P8
	3	P11, Ob

Tabel 6. Groepering van tobamovirussen uit tabak (WU1), aubergine (A1) en peper (FO, P14, SL, P8, P11 en Ob) op grond van hun reacties in Capsicum spp. en op grond van hun serologische verwantschappen.

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Samenvatting

Tobamovirussen uit peper, aubergine en tabak: een vergelijking met behulp van toetsplanten en serologie

Zes tobamovirussen uit peper (FO, Ob, P8, P11, P14 en SL) en één uit aubergine (A1) konden met behulp van toetsplanten alle van elkaar worden onderscheiden. In hun reacties in *Capsicum*-soorten, kwamen A1 en FO sterk overeen met elkaar en met het gewone tabaksmozaïekvirus (WU1). Ob, P11 en P8, die in dit opzicht onderling veel overeenkomst vertoonden, verschilden duidelijk van alle andere. Hetzelfde gold voor P14 en SL.

Ook met behulp van de micro-precipitatietoets konden de virusstammen in groepen worden ingedeeld. Groep I werd gevormd door WU1, groep II door A1, FO, P8, P14 en SL en groep III door P11 en Ob. Met behulp van ELISA kon groep II worden onderverdeeld in twee ondergroepen, namelijk A1 en FO enerzijds en P8, P14 en SL anderzijds.

De nauwe serologische verwantschap van A1 met FO is conform de grote overeenkomst in waardplantreacties. Hetzelfde geldt voor P11 en Ob, wanneer we alleen hun reacties in *Capsicum*-soorten beschouwen. P8 echter, die wat het laatste betreft meer op Ob en P11 lijkt, vertoonde serologisch meer overeenkomst met P14 en SL. WU1 verschilde serologisch zeer sterk van alle andere onderzochte virusstammen.

Geconcludeerd kan worden dat de waargenomen overeenkomst tussen de onderzochte virusstammen in hun reacties in *Capsicum*-soorten niet altijd gesteund wordt door hun serologische verwantschappen.

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