Turnip Mosaic Virus Strains in Southern Ontario, Canada

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ABSTRACT

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Four strains of turnip mosaic virus (TuMV) were identified throughout the vegetable-growing regions of southern Ontario. Virus infection was associated predominantly with cruciferous hosts, with the highest incidence of infection occurring in rutabaga (Brassica napus subsp. rapifera) and winter canola (B. n. subsp. oleifera) plantings. The most widespread TuMV strain, TuMV-SI, appears to be similar to the TuMV-C3 strain reported in New York State, whereas the prevalence of the other strains depended largely on the presence of specific hosts. A fifth strain of TuMV was isolated from rutabaga grown in Joliette, Quebec. Certain cultivars of rutabaga and Chinese cabbage (B. campestris subsp. pekinensis) were determined to be resistant or immune to the five strains of TuMV.

Additional keywords: differential host range, ELISA

Cole crops are among the most important vegetables grown in Ontario and in 1987 had a farmgate value of over \$50 million (Canadian). Although turnip mosaic virus (TuMV) is recognized to be the most widespread and important virus infecting cole crops worldwide, information is generally lacking on the extent and importance of this virus in Ontario. Previously, production losses caused by this virus have been restricted to rutabaga (Brassica napus L. subsp. rapifera (Metzg.) Sinsk.), in which infrequent epidemics have occurred (3,4). With the commercial introduction in the early 1980s of winter canola (B. n. subsp. oleifera (Metzg.) Sinsk.) into southern Ontario, however, the incidence of TuMV infection has increased sharply not only in rutabaga but also in other

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cruciferous crops (Ontario Rutabaga Growers Report to the Ontario Ministry of Agriculture and Food, 1985). In 1985, following a rapid increase in acreage of winter canola, severe production losses occurred in the rutabaga crop in southwestern Ontario. Within 2 yr, losses from TuMV were apparent in cabbage (B. oleracea L. subsp. capitata), Chinese broccoli (B. alboglabra L. H. Bailey), and Chinese cabbage (B. campestris L. subsp. pekinensis (Lour.) Rupr.) grown in outlying areas.

Previous studies have identified at least two strains of TuMV naturally occurring in southern Ontario (3,11). One of these strains, however, is not known to infect commercially grown Brassica crops. In New York State, three major strains of TuMV have been identified, all of which infect Chinese cabbage. No significant physical or serological differences have been shown among the various reported strains of TuMV (1,7,11). The following study was initiated in 1985 to examine the host range and strain distribution of TuMV across southern Ontario so that effective

recommendations on disease control and breeding strategies could be structured.

MATERIALS AND METHODS

Plant material. Seeds of Chinese cabbage were obtained from R. Provvidenti (New York State Agricultural Experiment Station, Cornell University, Geneva), Sakata Seed America, Inc. (P.O. Box 2805, San Francisco, CA), Shensi Academy of Agriculture Vegetable Institute (Wukum, Shensi Province, People's Republic of China), Stokes Seeds (P.O. Box 10, St. Catharines, Ontario), and Takii and Company Ltd. (C.P.O. Box 7, Kyoto, Japan). Rutabaga cultivars were obtained from Stokes Seeds and from J. A. Tomlinson (National Vegetable Research Station, Wellesbourne, Warwick, U.K.). Chinese cabbage and rutabaga cultivars used as differentials for virus strain identification were grown to the four- to six-leaf stage under greenhouse conditions (25 C) with supplementary high-pressure sodium vapor light (350 $\mu \text{ E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, 16-hr photoperiod). All greenhouses used in this study were maintained insect-free.

Virus isolates. TuMV-susceptible hosts were selected (Table 1) and samples were collected from both commercially grown cruciferous crops and field weeds in areas of southern Ontario where TuMV had been previously reported (Fig. 1). Foliar samples, accumulated during 1985-1987, were stored frozen (-65 C) until required. All samples were screened for TuMV by bioassay on Chenopodium quinoa Willd., and virus identity was confirmed by enzyme-linked immunosorbent assay (ELISA). TuMV from selected samples was passed through four successive single-lesion transfers in C. quinoa, and isolates subsequently were maintained in the rutabaga cultivar Laurentien; in the chinese cabbage cultivars China Express, China Pride, and Winter Giant; or in garlic mustard (Alliaria petiolata (M. Bieb.) Cavara & Grande). The TuMV-C1 and TuMV-C2 strains (7) were provided by R. Provvidenti and P. Williams (University of Wisconsin, Madison), respectively. The TuMV-C3 and TuMV-C4 strains were unavailable. The strain hereafter referred to as TuMV-S-5 was supplied by R. Doucet (Service de Recherche en Phytotechnie de Ste. Hyacinthe, Ministere de L'Agriculture des Pecheries et de L'Alimentiation, St-Hyacinthe, Quebec); the strain was obtained from rutabagas from a commercial field near Joliette, Quebec, in which the incidence of TuMV was high.

Strain evaluation. Leaf tissue from rutabaga and Chinese cabbage cultivars showing prominent TuMV symptoms was triturated (1:9, w/v) in phosphatebuffered saline (0.02 M phosphate, 0.15 M NaCl, pH 7.2) containing 0.5 ml/L of Tween 20, and the extracts were rubbed onto Carborundum-dusted leaves of four plants of each Chinese cabbage and rutabaga cultivar used for strain identification (Table 2). This host range is similar to the Chinese cabbage cultivars used by Provvidenti (7) in previous evaluation for resistance to TuMV strains. Inoculated leaves on each plant were marked, and plants were maintained in the greenhouse at 25 C for 15 days, then at 15 C for 15 days to promote symptom expression (8). Thirty days after inoculation, inoculated and uninoculated leaves from each cultivar were tested for virus by bioassay on C. quinoa and by ELISA. Differential hosts that remained symptomless and tested negative for virus were rated as highly resistant or immune, those in which virus was detected only in inoculated leaves were classified as resistant, those that developed mild or transitory systemic symptoms were considered tolerant, and those that showed moderate to severe systemic mosaic, necrosis, or stunting were regarded as susceptible.

After strain identification, the host range screening was expanded. Six plants of each of the following were mechanically inoculated with each virus strain: (Amaranthaceae) Gomphrena globosa L.; (Chenopodiaceae) Beta vulgaris L. 'White King,' Chenopodium amaranticolor Coste & Reyn., C. quinoa; (Compositae) Lactuca sativa L. 'Premier'; (Cruciferae) A. petiolata, B. o. subsp. capitata 'Polar Express,' B. o. subsp. botrytis L. 'Dominant,' B. o. subsp. gemmifera DC. 'Jade Cross,' B. o. subsp. italica Plenck 'Packman'; (Cucurbitaceae) Cucumis sativus L. 'Improved Long Green'; (Leguminosae) Phaseolus vulgaris L. 'Frenchie,' Vigna unguiculata L. Walp. 'Queen Anne Blackeye'; and (Solanaceae) Capsicum annuum L. 'Early Hybrid,' Datura stramonium L.,

Lycopersicon esculentum Mill. 'Glamour,' Nicotiana glutinosa L., N. tabacum L. 'Harrow Velvet,' and Petunia × hybrida (Vilm.) 'Calypso.' Plants were maintained under greenhouse conditions for 3 wk, at which time virus symptoms were recorded and virus presence determined by ELISA.

ELISA. The direct double-antibody sandwich ELISA was used for virus detection, as described by Clark and Adams (2). Initially, a polyclonal antiserum (11) prepared against TuMV in the rutabaga cultivar Laurentien was used, but absorbance baselines to sap from healthy plants varied widely with different cultivars and lower sensitivity made the antiserum less suitable than the monoclonal antiserum (14) subsequently used. The monoclonal antiserum had a titer of 1:1,024, as determined by the

sodium dodecyl sulfate/agar doublediffusion test (8). All tests were done in Immulon 2 flat-bottom Removawell plates (Dynatech Laboratories, Chantilly, VA), with 200 μ l of reagent used for each of the four steps. Wells were coated with purified TuMV immunoglobulin at 1 $\mu g/ml$ in 0.05 M sodium carbonate buffer, pH 9.6 (1:1,000, v/v, 4 hr, 38 C). After washing, 200 μ l of tissue triturates (tissue:ELISA extraction buffer, 1:19, w/v) was loaded into three replicate wells for each sample and plates were incubated for 4 hr at 38 C. Alkaline phosphatase (Type 7, Sigma Chemical Co.) conjugated to TuMV IgG at an enzyme:protein ratio of 2.5:1 (v/v) was added for 3 hr at 38 C. Substrate reactions were stopped by adding $50 \mu l$ of 3 M NaOH, and the absorbance was measured at 405 nm in an Eurogenics

Table 1. Field collection samples used for differentiation of turnip mosaic virus strains in Ontario

	No. sites	No. samples	Positive samples		
Host	sampled	collected	No.	%	
Amaranthaceae					
Amaranthus caudatus L. (amaranth)	12	44	0	0	
Begoniaceae					
Begonia L. (begonia)	31	31	0	0	
Chenopodiaceae					
Beta vulgaris L. (beet)	20	42	16	38	
B. v. subsp. cicla (L.) Koch (chard)	14	24	0	0	
Chenopodium album L. (lambsquarters)	29	59	2	3	
Spinacia oleracea L. (spinach)	17	17	4	24	
Compositae					
Cichorium endivia L. (endive)	20	20	0	0	
Lactuca sativa L. (lettuce)	20	20	4	20	
Sonchus oleraceus L. (sowthistle)	30	42	8	19	
Tagetes erecta L. (marigold)	10	14	6	43	
Zinnia elegans Jacq. (zinnia)	19	22	8	36	
Cruciferae					
Alliaria petiolata (M. Bieb.)					
Cavara & Grande (garlic mustard)	48	145	132	91	
Brassica alboglabra L. H. Bailey					
(Chinese broccoli)	6	10	2	20	
B. campestris L. subsp. pekinensis					
(Lour.) Rupr. (Chinese cabbage)	18	207	98	47	
B. napus L. subsp. oleifera					
(Metzg.) Sinsk. (canola)	48	302	108	36	
B. n. subsp. rapifera					
(Metzg.) Sinsk. (rutabaga)	52	1,547	1,121	72	
B. oleracea L. subsp. botrytis L.		ŕ			
(cauliflower)	20	82	12	15	
B. o. subsp. capitata L. (cabbage)	30	32	8	25	
B. o. subsp. gemmifera DC.					
(Brussels sprout)	18	28	0	0	
B. o. subsp. italica Plenck					
(broccoli)	13	13	2	15	
B. rapa L. (mustard)	48	183	21	11	
Hesperis matronalis L.					
(dame's rocket)	14	48	9	19	
Raphanus sativus L. (radish)	8	16	0	0	
R. s. subsp. longipinnatus					
L. H. Bailey (Chinese radish)	4	9	3	33	
Cucurbitaceae					
Cucumis sativus L. (cucumber)	32	32	0	0	
Cucurbita pepo L. (marrow)	4	4	3	75	
Geraniaceae	•	•			
Geranium L. (geranium)	18	18	0	0	
Solanaceae	••		•	-	
Petunia × hybrida Hort. Vilm.					
(petunia)	47	47	5	11	
	57	114	0	0	
Assorted weeds					

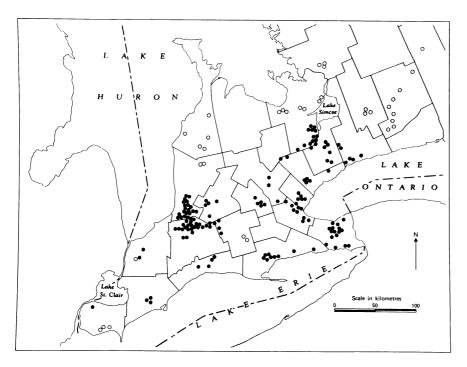


Fig. 1. Sites of turnip mosaic virus sample collections across southern Ontario during 1985–1987.
= Samples positive and o = samples negative for TuMV.

Table 2. Reactions of cultivars of rutabaga (Brassica napus subsp. rapifera) and Chinese cabbage (B. campestris subsp. pekinensis) to mechanical inoculation with strains of turnip mosaic virus (TuMV)

Source Cultivar ^a	Origin of germ plasm ^b	Reactions of TuMV strains ^c						
		S1	S2	S3	S4	S-5	C1	C2
National Vegetable Research Station, U.K.								
Calder*	U.K.	I	I	I	I	I	I	I
Line 165*	U.K.	T	I	T	I	I	I	I
Sensation*	U.K.	I	I	I	I	Ī	Ī	Ī
N.Y. State Agricultural Experiment Station							_	_
PI 391560 (Er-pao-tou)	C	I	I	I	I	I	I	R
PI 419105 (Peking-hsiao-tsing-kou)	C	R	Ī	R	Ī	Ī	ŝ	R
PI 419106 (Pao-tou-tsing)	C	I	Ī	R	Ī	Ī	Ť	R
Sakata Seed America, Inc.					_	_	_	
China Express	J	S	S	S	S	I	S	S
Early Jade Pagoda	J	S	S	Š	Š	Î	Š	S
Spring Triumph	J	Š	Š	S	Ř	Î	Š	Š
Tropical Delight	Ĵ	Š	Š	Š	S	Ì	Ĭ	Š
Tropical Pride	Ĵ	Š	S	S	Š	Ī	ŝ	S
Winter Champion	J	Š	Š	Š	Ř	Î	Š	Š
Winter Giant	J	Š	Š	Š	S	î	Ĭ	S
Shensi Academy of Agriculture	-	~	_	_	_	•	•	
PI 418957 (5241)	С	I	I	I	I	I	I	R
Stokes Seeds	_	-	-	-	•	•	•	• •
China Pride	J	S	S	S	S	I	S	S
Jade Pagoda	Ĵ	Š	Š	S	Š	î	Š	S
Kasumi	J	Š	Š	Š	Š	Î	Š	Š
Laurentien*	J	Š	Ĭ	Š	Š	i	Š	Ĭ
Michihli	Ĵ	S	Ś	Š	Š	Î	S	Ť
Monument	J	Š	S	R	Š	Î	S	ŝ
Springtime	J	Š	S	S	Š	Î	S	S
Summertime	J	S	S	S	S	Î	S	S
Wintertime	Ĵ	Š	Š	Š	Š	î	Š	S
Takii and Company Ltd.	3	J					5	5
Blues	J	S	S	S	S	I	S	S
Crusader	J	Š	I	S	S	Ï	S	R
Hero	Ĵ	Š	ŝ	S	S	Í	S	R
Tango	J	Š	Š	S	S	Ï	S	S
50 Days	J	Š	S	Š	S	Ì	S	S

^a* = Rutabaga cultivars; all others are Chinese cabbage cultivars.

MPR-A4 microplate reader (Diamed Laboratory Supplies Inc., Mississauga, Ontario). Test samples were considered positive if absorbance values exceeded twice those of healthy control samples.

RESULTS AND DISCUSSION

TuMV was widespread across most of the vegetable-growing areas of southern Ontario during 1985–1987 (Fig. 1). The highest incidence of virus was generally associated with rutabaga and winter canola plantings. Many of the Cruciferae hosts, while indexing positive for virus, showed high levels of tolerance and generally only mild symptoms. TuMV was not confined to cruciferous crops but included crops and weeds of the families Chenopodiaceae, Compositae, Cucurbitaceae, and Solanaceae (Table 1).

Isolates of TuMV from plants collected from across the province were segregated into four distinct virus strains (S1, S2, S3, and S4), based on the symptoms and invasiveness in the Chinese cabbage/rutabaga differential series (Table 2). A fifth strain, TuMV-S-5, was identified from rutabaga received from Quebec, the second largest producer of rutabagas in Canada.

The most prevalent strain, TuMV-S1, was isolated from rutabaga, winter canola, cabbage, and several species of field mustards within the rutabagagrowing region of Huron, Middlesex, and Perth counties. This strain also was present in most of the vegetable- and winter canola-growing areas across southern Ontario (Fig. 2) and was the most aggressive of the five Canadian strains examined, systemically infecting most of the Chinese cabbage and rutabaga cultivars tested (Table 2). Comparison of this strain with the British strain isolated from swede (15) in winter canola cultivars similarly demonstrated a wider cultivar susceptibility to the TuMV-S1 strain (10,15). The TuMV-S1 strain appears to be similar to the TuMV-C3 strain isolated from turnip in New York State (7), on the basis of its reaction to the Chinese cabbage and rutabaga differentials. Because of the geographic proximity of these two vegetablegrowing areas, and because over 65% of the rutabagas from southwestern Ontario. many infected with TuMV, are exported to U.S. markets, it is not surprising that these two isolates are similar.

The TuMV-S2 strain, isolated from Chinese cabbage, was found only in south-central Ontario, where most of the Chinese vegetable production is located (Fig. 2). This strain showed a more restricted host range, being limited to several of the Chinese cabbage cultivars, and did not infect the rutabaga cultivar (Table 2). The S2 strain also was found in field plantings of Chinese broccoli (guy lon), Chinese radish (lo bok), and mustard cabbage (bok choy or pak-choi). The strain is less aggressive than the

^bU.K = United Kingdom, C = People's Republic of China, J = Japan.

 $^{^{}c}I = immune, R = resistant, T = tolerant, S = susceptible.$

TuMV-C2 strain isolated from Chinese cabbage in New York State (7). Chinese cabbage cultivars obtained from the People's Republic of China were immune to the Ontario TuMV-S2 strain but resistant to the New York State TuMV-C2 strain.

The TuMV-S3 strain isolated from cauliflower was similar to the TuMV-S1 strain. The Chinese cabbage line PI 418957 and the cultivar Monument, however, were both hypersensitively resistant to the S3 strain and immune to the S1 strain. In this respect, there was no similarity with the TuMV-C1 strain isolated from cabbage in New York State (7).

The TuMV-S4 strain, isolated from A. petiolata, did not infect rutabaga or Chinese cabbage cultivars. As reported previously (11), natural infection is limited to Hesperis matronalis L. and A. petiolata, which are prevalent in the southern part of the province. Between 1985 and 1987, this strain was consistently isolated from most A. petiolata samples obtained across southern Ontario (Fig. 2). Contrary to some disease control recommendations (5), control of weeds such as H. matronalis will not reduce the incidence of TuMV in commercially grown Brassica hosts, since the virus is restricted in its host range to only a few weed hosts and does not infect commercially grown cruciferous crops.

The TuMV-S4 strain was less aggressive than the TuMV-S1 or TuMV-S3 Ontario isolates infecting rutabaga. Selection 165, a rutabaga breeding line immune to a British strain of TuMV (13) and tolerant to the Ontario TuMV-S1 isolate of TuMV, was immune to TuMV-S-5, whereas two of the Chinese cabbage cultivars showed resistance to that strain.

Cultivars immune to all five Canadian strains of TuMV were Calder and Sensation of rutabaga and PI 391560 and PI 418957 of Chinese cabbage. PI 419105 was hypersensitively resistant to both TuMV-S1 and TuMV-S3, whereas PI 419106 was immune to all strains except TuMV-S3, where hypersensitive local lesions formed on inoculated leaves. Most TuMV strains produced severe systemic necrosis on Chinese cabbage cultivars, with varying degrees of systemic foliar mottle. Petiolar browning, chlorosis, and stunting were common among most of the cultivars systemically infected with virus. As observed by Provvidenti (7), resistance or immunity to TuMV was more common among the Chinese cabbage cultivars from China than among those from Japan. No immunity or resistance to TuMV-S1 was found among the Japanese cultivars, which represent the major source of seed commercially available to the Ontario farming community.

When the TuMV strains were examined on a broader host range used to characterize the TuMV type strain (12,13),

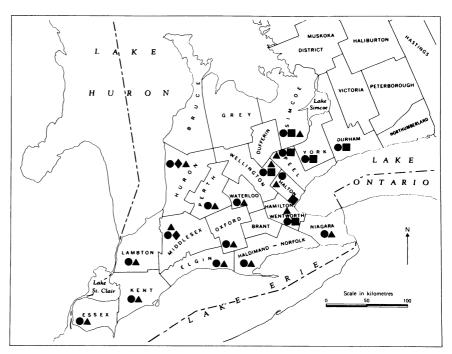


Fig. 2. Turnip mosaic virus strain distribution in counties of southern Ontario during 1985–1987. • = Strain S1, ■ = strain S2, ◆ = strain S4.

all the Canadian isolates were basically similar to the type strain. Indicator plants immune to all five Canadian strains of TuMV were B. vulgaris, L. sativa, B. o. subsp. gemmifera, B. o. subsp. italica, C. sativus, P. vulgaris, V. unguiculata, C. annuum, D. stramonium, and L. esculentum. All the TuMV strains systemically infected P. hybrida and, with the exception of TuMV-S2, TuMV-C2, and TuMV-S4, produced mild mosaic or chlorotic lesions on B. o. subsp. botrytis and B. n. subsp. oleifera. Chlorotic or necrotic local lesions were produced by all strains on C. quinoa, C. amaranticolor, G. globosa, and N. tabacum. All strains except TuMV-S4 produced diffuse chlorotic or small necrotic lesions on N. glutinosa and mild mosaic mottle on B. c. subsp. capitata, indicating that they are more closely related to the TuMV common strain group than to the cabbage strain group (16).

This study has shown that four strains of TuMV are common in Ontario, three of which infect commercially grown cruciferous crops. This and previous evaluations of rutabaga cultivars for TuMV resistance (9) have identified rutabaga cultivars Calder and Sensation as being immune to all the TuMV strains identified in Ontario. These cultivars represent valuable TuMV-resistant germ plasm for cruciferous breeding programs. Similarly, the Chinese lines of Chinese cabbage showed either hypersensitive resistance or immunity to all the Canadian TuMV strains and might become potentially useful for intraspecific or interspecific gene transfers (7).

Geographically, most of the strains overlapped in southern Ontario. The

prevalence of each strain was related more to the presence of a specific host crop(s) or weed(s) than to the introduction of a specific strain within different localities. Finding the TuMV-S2 strain only in south-central Ontario does not preclude the possibility of it occurring in other areas after the introduction of Chinese vegetables. Similarly, the TuMV-S1 strain, already present across most of southern Ontario, would readily infect Chinese vegetables after their introduction into areas where TuMV-S1 is prevalent. With Chinese vegetables being considered as a transitional crop in Ontario (6), expansion in acreage is likely to occur over the next few years. Thus, introduction of Chinese vegetables into rutabaga- or winter canola-growing areas is highly inadvisable. Furthermore, the rapid expansion in acreage of winter canola across southern Ontario presents an increasing threat to many cruciferous crops, in that it provides an overwintering reservoir for the TuMV-S1 and TuMV-S3 strains. The wide host range of these strains emphasizes the importance of incorporating TuMV resistance into most commercially grown cruciferous crops. The identification of several germ plasm lines resistant or immune to the indigenous virus strains will permit the development of polygenic resistant cultivars.

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