Turnip Mosaic Virus Strains in Cruciferous Hosts in Taiwan

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ABSTRACT

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An islandwide survey of the major vegetable production areas of Taiwan was conducted to determine the presence, distribution, and prevalence of strains of turnip mosaic virus (TuMV) affecting Chinese cabbage (*Brassica campestris* subsp. *pekinensis*), radish (*Raphanus sativus*), and smooth-leaf mustard (*B. juncea*). In addition to the four strains of the virus described in the United States, a fifth strain (TuMV-C5) was found that is capable of systemically infecting the multiresistant Chinese cabbage PI 418957. The physical and serological properties of strain C5 were indistinguishable from the other strains except for its low absorbance values in enzyme-linked immunosorbent assay. TuMV-C4 appeared to be the most widespread strain, followed in decreasing prevalence by C2, C3, C5, and C1. Resistance to TuMV-C5, as well as to the other four strains, was found in plants of the Chinese cabbage line AVRDC Acc. 730.

Turnip mosaic virus (TuMV) is geographically widespread and has been reported in North America (2,19–21,26), Europe (3,24,25), Africa (14), Asia (1,5–9,13,17,18,23,27,28), and Australia and New Zealand (4,12). In contrast to cauliflower mosaic virus, which is confined to cruciferous crops, TuMV has a wide natural host range, which includes not only many members of the genus *Brassica* but also legumes (9,14,19) and ornamental plants belonging to different families (21,25,26). In Asia, TuMV is considered the most important virus of cultivated cruciferous cash crops such as Chinese cabbage, radish, and smooth-leaf mustard and has caused significant yield losses (23). Resistance is considered the only effective means of control, and programs aimed at finding TuMV-resistant cultivars and breeding stock have been initiated in several countries of Asia (6,16,18,23).

Provvidenti (21) recently suggested that resistance to TuMV in Chinese cabbage is strain-specific and that several independently inherited genes for resistance are involved. He isolated four strains of the virus in cabbage, Chinese cabbage, and turnip in New York State. After screening 46 Chinese cabbage cultivars of Japanese and Chinese origin for resistance to TuMV-C1, C2, and C3, he observed that TuMV resistance in Chinese cabbage varied with its origin. Most Japanese cultivars were immune or resistant to TuMV-C1, but Chinese cultivars were more often resistant to C2.

Resistance to C3 and C4 was found only in Chinese cultivars. This clearly demonstrates the importance of using all available strains of TuMV in any program aimed at developing cultivars with durable TuMV resistance. With this in mind, a survey was initiated in 1982 (15) to determine the presence and prevalence of TuMV strains infecting commercially grown cruciferous vegetables in Taiwan and to use those strains for the development of stable yielding, disease-resistant, and heat-tolerant Chinese cabbage cultivars in the breeding program of the Asian Vegetable Research and Development Center (AVRDC).

MATERIALS AND METHODS

Leaves of field-grown Chinese cabbage (*Brassica campestris* subsp. *pekinensis* L.), radish (*Raphanus sativus* L.), and smooth-leaf mustard (*B. juncea* (L.) Cosson) were collected during 1982–1983 from the major vegetable-growing areas of Taiwan, including AVRDC. TuMV was isolated by sap inoculation to *Nicotiana tabacum* L. 'White Burley,' a nonhost for cauliflower mosaic virus, radish enation mosaic virus, turnip crinkle virus, and turnip yellow mosaic virus. Before they were used for determination of morphology, host range, physical properties, and serology, each isolate of TuMV was passed through three successive single local lesion transfers on *Chenopodium amaranticolor* Coste & Reyn. All isolates were maintained in a very susceptible local variety of *B. juncea.*

For host range studies, at least four test plants of each species or cultivar belonging to the families Cruciferae, Chenopodiaceae, Amaranthaceae, Compositae, Ficoidaceae, Solanaceae, Lamiaceae, Cucurbitaceae, Balsaminaceae, and Leguminosae were inoculated.

For strain differentiation, four of nine Chinese cabbage cultivars, PI 418957, PI 41905, Tropical Delight, and Crusader, used by Provvidenti (20) for TuMV strain classification were chosen for their ability to differentiate the four strains. Ten plants of each cultivar were inoculated with each TuMV isolate. After inoculation, all plants were maintained in an artificially lighted, controlled-environment growth room (12-hr photoperiod, day temperature 26 C, night temperature 20 C). Back-inoculations to *C. amaranticolor* were made 4 wk after inoculation to confirm presence of the virus. Particle morphology was determined from leaf preparations of systemically infected *B. juncea* tissues, diced in 2% uranylacetate, and examined in an electron microscope.

The dilution end point (DEP) was determined by serial dilutions of crude sap of infected *B. juncea* in 0.01 M phosphate buffer, pH 7.0. The thermal inactivation point (TIP) was tested by immersing 1-ml samples of crude sap in a water bath of a given temperature for 10 min, followed by rapid cooling under running tap water. For longevity in vitro (LIV), crude extracts were incubated at 25 C. Infected *B. juncea* leaves served as the virus source and *C. amaranticolor* was used as the local lesion assay host.

TuMV-C5 was purified from systemically infected leaves of *B. juncea* Acc. B96 following the method of Choi et al (10). For antiserum production, rabbits were given at weekly intervals four intramuscular injections of a purified virus preparation emulsified in Freund's incomplete adjuvant. The resulting antiserum had a titer of 1:64 in sodium dodecyl sulfate (SDS) agar gel double-diffusion test (22). Serological tests, using partially purified antigens from systemically infected mustard leaves, were done by double-antibody sandwich enzyme-linked immunosorbent assay (ELISA) as described by Clark and Adams (11).

Gamma globulins and enzyme-conjugated gamma globulins prepared from antiserum to a German isolate of TuMV (cabbage blackring strain) were obtained from H. J. Vetten (BBA Braunschweig, West Germany). The gamma globulins from antiserum to a Japanese isolate of TuMV (obtained from N. Sako, Saga University, Japan) and from antiserum to the Taiwan TuMV-C5 strain were partially purified by precipitation with ammonium sulfate

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and were further purified by passage through a DEAE-cellulose column. The gamma globulin fractions were pooled and conjugated (15:1, v/v) with alkaline phosphatase (grade 1, from calf intestine, Boehringer Co., Mannheim, West Germany) using 0.06% glutaraldehyde as the coupling agent. The conjugate was used at a dilution of 1/500. Coating, antigen addition, and conjugate addition were done for 4 hr at 30 C, 18 hr at 4 C, and 5 hr at 30 C, respectively. Substrate hydrolysis time was 1 hr at room temperature. At each step, 200-μl aliquots of reactants were used. Triplicate wells were run for each sample and mean values were used for comparisons. Absorbances at 405 nm were measured directly from the plate with a Titertek Multiscan photometer (Flow Laboratories Inc., McLean, VA). Results were considered positive for test samples if the average absorbance at 405 nm was twice that of healthy control samples in the same plate.

RESULTS

Isolation of the virus. On the basis of host reactions, particle length and shape, and serological tests, TuMV was present in all nine vegetable production areas surveyed and was isolated from 52 of the 102 leaf samples collected from Chinese cabbage, radish, and mustard. After inoculation of the four TuMV strain differentials, the isolates could be grouped into five groups, representing all four TuMV strains described by Provvidenti (20) and a fifth strain of TuMV that could systemically infect *B. campestris* subsp. *pekinensis* PI 418957. Provvidenti had found this accession immune to TuMV-C1 and C3 and resistant to the other two strains isolated in the United States (Table 1). This new strain, tentatively named TuMV-C5 (15), has only been found in AVRDC fields on Chinese cabbage and mustard.

TuMV strain C1 was found only twice in two locations in southern Taiwan (Table 2). Nine isolates were typed C3, 12 isolates were strain C2, and 24 were C4. Strain C2 was present in four of the nine locations surveyed, strain C3 in six, and strain C4 in eight locations.

Host reactions. Of the 88 plant species tested in the host range study, 57 were susceptible to one or several strains of TuMV (Table 3).

Plants immune to all five strains of the virus were Cruciferae: *Brassica oleracea* subsp. *capitata* 'Cia-chio' and 'Hitoma,' *B. oleracea* subsp. *italica* (unidentified local variety), and *B. caulorapa* 'Grand Duke'; Chenopodiaceae: *Beta vulgaris* 'Eckendorfer Gelbe'; Compositae: *Lactuca sativa* 'Celtuce'; Solanaceae: *Capsicum annuum* 'Tobasco,' *Datura stramonium*, *Lycopersicon esculentum* 'Perou,' and *Solanum melongena* 'Pintung Long'; *Nicotiana sylvestris*; Lamiaceae: *Ocimium basilicum*; Cucurbitaceae: *Cucumis sativus* 'National Pickling,' and *C. melo* 'Charentais'; Amaranthaceae: *Amaranthus mangostanus*; Leguminosae: *Glycine max* 'Bragg,' *Medicago sativa* 'Maxidor,' *Phaseolus vulgaris* 'Pinto' and 'Saxa,' *Pisum sativum* 'Dark Skin Perfection,' *Vicia faba*, *Vigna radiata* 'AVRDC Acc. V2010,' and *V. unguiculata* 'Blackeye.'

Hosts that were systemically infected by all five strains were *Spinacia oleracea* 'ORO 1265,' 'Vicking,' 'Bloomsdale Long Standing,' and *Petunia hybrida*. *N. clevelandii* gave local lesions on the inoculated leaves in addition to systemic mosaic and necrosis. On *Chenopodium quinoa*, all five strains produced local and systemic lesions as well as mosaic.

Local lesion hosts to all five strains were *C. amaranticolor*, *Gomphrena globosa*, and *N. tabacum* 'Samsun,' 'Xanthi,' and 'White Burley.' *Tetragonia expansa* reacted with local chlorotic ring spots.

Most TuMV strains produced severe symptoms on Chinese cabbage, paitsai, rape, mustard, and radish. The following types of reactions were observed on these hosts: chlorotic or necrotic local lesions, severe mosaic, necrosis, and leaf deformation. *B. campestris* subsp. *chinensis* 'Small Paitsai,' 'Green Petiole Paitsai,' *B. campestris* subsp. *rapa* 'Presto,' *B. juncea* 'AVRDC Acc. B96,' *B. napus*, and *Raphanus sativus* subsp. *niger* 'Meilong Early' were systemically infected by all five strains.

In Chinese cabbage, susceptibility to all strains except TuMV-C1 appears to be common. Of the 14 cultivars tested, 11 were immune to strain 1.

Brassica species with $n = 9$ chromosomes, such as common cabbage, cauliflower, broccoli, and kohlrabi, were frequently found immune to all five TuMV strains or to strains C1 and C2. Some cultivars were susceptible to strains C3, C4, and C5, which produced chlorotic local lesions on the inoculated leaves and mild mosaic symptoms. Chlorotic ring spots were observed only twice on two cultivars of cauliflower. No necrotic ring spots were produced.

In vitro properties. The TIP of all five strains was between 60 and 65 C; the DEP was between 10^{-4} and 10^{-5}. Infectivity of TuMV-C2, C3, and C4 at 26 C was lost within 4–5 days, that of C5 within 6–7 days, and that of C1 within 8–9 days.

Serology. In ELISA, all five strains of TuMV isolated on Taiwan reacted positively with antiserum to the cabbage black ring strain of TuMV (Taiwan isolate), to a Japanese isolate of TuMV (4), and to TuMV-C5 (Table 4).

DISCUSSION

In his attempt to group all reported TuMV isolates on the basis of host range, disease symptoms, and locality, Yoshii (28) was able to distinguish two strain groups, the cabbage strain group, which produced severe necrotic ring spots on *B. oleracea* subsp. *capitata* and severe mosaic on *N. glutinosa*, and the common strain group, which produced only mild symptoms on these two hosts.

Table 1. Effects of five groups of Taiwan turnip mosaic virus (TuMV) strains on *Brassica campestris* subsp. *pekinensis* cultivars selected for strain differentiation

	Reaction[a]				
Host	**Group 1**	**Group 2**	**Group 3**	**Group 4**	**Group 5**
Tropical Delight	−/−(I)	CL/M,N,LD(S)	CL/M,N(S)	CL/M,N(S)	CL/M,N(S)
Crusader	L/M(S)	L/−(R)	L/M(S)	L/M(S)	L/M(S)
PI 418957	−/−(I)	L/−(R)	−/−(I)	L/−(R)	L/VC,M(S)
PI 419105	L/M(S)	L/−(R)	L/−(R)	L/M(S)	L/M(S)

[a] Format for symptom symbols: reaction on inoculated leaves/reaction on uninoculated leaves. CL = chlorotic lesions, M = mosaic, N = systemic necrosis, VC = veinclearing, LD = leaf deformation, L = latent infection, − = symptomless (no virus recovered by back-inoculation to *Chenopodium amaranticolor*), I = immune, R = resistant, and S = susceptible.

Table 2. Presence of turnip mosaic virus (TuMV) strains on Chinese cabbage and other cruciferous vegetables in the major Chinese cabbage production areas of Taiwan

		TuMV strain				
Location	**Number of samples collected**	**C1**	**C2**	**C3**	**C4**	**C5**
North Taiwan						
Yang-Ming-Shan	3	···	···	1[a]	1	···
Lu-Chou	3	···	···	1	2	···
Chu-Pei	6	···	···	···	1	···
Chon-Lin	7	···	1	···	1	···
Central Taiwan						
Chiu-Ho	8	···	···	1	2	···
Yong-Chin	6	···	1	1	2	···
South Taiwan						
Chia-Yi	14	1	3	1	5	···
Fengshan	1	1	···	···	···	···
Shanhua (AVRDC)	54	···	7	4	10	5
Total	102	2	12	9	24	5

[a] Number of samples infected.

The TuMV isolates from Taiwan produced mild symptoms on *N. glutinosa* and on *B. campestris* subsp. *capitata*, indicating they all belonged to the common strain group. Yoshii (28) also found a distinct difference in the geographic distribution of the two strain groups. Isolates of the common strain group occurred worldwide, whereas isolates of the cabbage strain group were confined to Europe, America, and Australia. The latter had never been found in Asian countries, where the common strain is found exclusively. Our investigation further supported this finding.

The TuMV isolates from Taiwan were further classified on the basis of differential host reactions on a select group of *B. campestris* subsp. *pekinensis* cultivars chosen from Provvidenti's TuMV strain differentials (20). They represented five strains of TuMV. The physical and serological properties of TuMV-C5 could not be distinguished clearly from those of the other four strains; however, ELISA absorbance values of strain C5 were consistently lower than those of the other four strains. Although the LIV of TuMV-C5 was slightly higher than that of most other strains, it was not higher than that of C1, which was 8–9 days. In their attempt to group eight TuMV isolates from rape, radish, turnip, and iris on the basis of their physical and serological properties and electrophoretic mobility, Choi et al (9) also failed to show any meaningful differences among the different isolates.

Strain TuMV-C4, which Provvidenti detected only once on Chinese cabbage in New York, appears to be widely distributed in Taiwan. It is not unreasonable to assume that TuMV-C5 has differentiated from TuMV-C4, the common strain in Taiwan, and that other strains may derive or have already derived from the five TuMV strains detected so far in Taiwan. The occurrence of additional strains or pathotypes infecting cruciferous crops is possible and further studies for their detection are needed. Some TuMV isolates have been reported (6,14,19) that are able to infect *Pisum sativum*, *Phaseolus vulgaris*, *Trifolium incarnatum*, and *Vicia faba*. It is likely that these are different

Table 3. Host range of five Taiwan strains of turnip mosaic virus (TuMV)

Host	Reaction[a]				
	TuMV-C1 (T-61)[b]	TuMV-C2 (T-37)	TuMV-C3 (T-40)	TuMV-C4 (T-91)	TuMV-C5 (T-42)
Cruciferae					
Brassica campestris subsp. *pekinensis*					
Hiratsuka No. 1	−/−	L/M,N,LD	L/VC,M,N,LD	L/VC,M,D	L/VC,M,N
Shimoyama Chitose	−/−	L/M	L/M	L/VC,M	L/VC,M
Kasumi	−/−	L/M	L/VC,M	L/VC,M,N	CL/VC,M,N
Shin Ju	−/−	CL/CC,M	VC/M,N	VC/VC,M,N	CL/CL,M,N
Nozaki Cross No. 1	L/M	L/M,LD	L/M,LD	L/M,LD	L/M,LD
No. 2	L/−	CL/M	CL/CL,M	L/M	L/M
No. 3	−/−	CL/M	CL/CL,M	L/M	L/M
Ping Luh	−/−	CL/M	L/M	CL/CL,M	L/M
AVRDC Acc. 204	−/−	CL/M,N or −/−	L/M	CL/M	L/M,N
AVRDC Acc. 205	−/−	CL/CL,M	CL/M	L/M	L/M
F_2 PI 419069	L/−	L/−	L/−	L/−	L/− or L/L
Line 8247	−/−	−/−	−/−	L/M	CL/CL,M
Tropicana	−/−	−/−	−/−	CRS/M or −/−	L/M or −/−
AVRDC Acc. 730	−/−	−/−	−/−	−/−	L/M or −/−
B. nigra					
Yellow flower	CS/M	−/M	−/M	−/CL,M	−/CL,M
White flower	CS/−	CS/M	CS/−	CS/−	CS/−
B. oleracea subsp. *capitata*					
Musca	CL/−	−/−	−/−	−/−	CL/M
Phoenix	−/−	−/−	−/−	−/−	CL/M
Bislet	−/−	−/−	−/−	CL/M	CL/M
Hidena	−/−	−/−	−/−	CL/M	CL/M
Tohshun As	−/−	−/−	CL/M	CL/M	CL/M
CM	−/−	−/−	−/−	CL/M	CL/M
B. oleracea subsp. *botrytis*					
45 Days Extra Early	−/−	−/−	−/−	CL/CRS	−/−
Fengshan Extra Early	−/−	−/−	−/−	L/M	−/−
Farmers Early	−/−	−/−	CRS/−	−/−	CL/−
Compositae					
Chichorium endivia					
Broad Leaved Batavian	CL/CL,M	−/−	−/−	CL/CL,M	−/−
Green Curled	L/−	−/−	−/−	−/−	−/−
Zinnia elegans					
Torch	CL/CL,M	CL/CL,M	L/M	CL/CL,M	CL/CL,M
Helianthus annuus	CS/M	−/−	−/−	−/−	−/−
Solanaceae					
Nicotiana glutinosa	CS/−	CS/−	CS/-	CS/CS	CS/CS
N. rustica	−/−	CL/−	CL/−	CL/−	CL/−
Physalis floridana	CS/L	CL/CL,M,LD	CL/CL,M,LD	CL/CL,M,LD	CL/CL,M,LD
Balsaminacae					
Impatiens balsamina					
Royal Mixed Colors	L/L	L/M	−/−	CL/M	CL/M

[a] Format for symptom symbols: reaction on inoculated leaves/reaction on uninoculated leaves. NL = necrotic lesions, CL = chlorotic lesions, CS = chlorotic spots, LD = leaf deformation, M = systemic mosaic, VC = veinclearing, N = necrosis, CRS = chlorotic ring spots, L = latent infection, − = symptomless (no virus recovered by back-inoculation to *Chenopodium amaranticolor*).

[b] Strains T61, T37, T40, T91, T42, representing strain groups 1, 2, 3, 4, and 5, respectively.

Table 4. Absorbance values obtained with five Taiwan turnip mosaic virus (TuMV) strains in enzyme-linked immunosorbent assay with antisera to three virus isolates

Immunoglobulin	Absorbance $A_{405\ nm}$[a]					
	Healthy[b]	TuMV-C1	TuMV-C2	TuMV-C3	TuMV-C4	TuMV-C5
German TuMV isolate[c]	0.004	1.585	1.674	0.836	1.788	0.242
Japanese TuMV isolate[d]	0.001	1.804	>2.000	1.279	>2.000	0.253
Taiwan TuMV (strain C5)[e]	0.052	1.812	1.480	0.761	1.834	0.365

[a] Means of absorbance ($A_{405\ nm}$) readings representing triplicate wells.
[b] Healthy *Brassica juncea* tissue.
[c] Coating gamma globulin 1 mg/ml, dilution 1/1,000.
[d] Coating gamma globulin 0.23 mg/ml, dilution 1/500.
[e] Coating gamma globulin 0.34 mg/ml, dilution 1/500.

pathotypes from the ones discussed here, because none of our five strains was able to infect any leguminous hosts.

The results of our host range study and of recent screening of AVRDC Chinese cabbage accessions and breeding lines (16) for resistance to strain C4 and C5 indicate that resistance or immunity to these two strains is not commonly found in Chinese cabbage. We have so far identified only one line, AVRDC Acc. 730, that carries immunity to all five strains of TuMV (Table 3). This line did, however, include a small percentage of individual plants susceptible to TuMV-C5, indicating this cultivar was not genetically pure.

The resistance to the five TuMV strains in Acc. 730 will be investigated further to determine the mode of inheritance of the genetic factor(s) involved and assess their potential for use as a source of resistance for AVRDC's Chinese cabbage improvement breeding program.

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