Cucumber Mosaic Virus in Weed Hosts Near Commercial Fields of Lettuce and Celery

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ABSTRACT

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Cucumber mosaic virus (CMV) was detected in 12 of 66 weed species collected during 1972 and 1973 in the vicinity of lettuce fields in Oswego County and celery fields in Orange County, New York. This is the first report of (i) natural infection by CMV for five* of the species and (ii) natural infection for three+ of the species in the United States. Final determination of CMV was based on the reaction of the isolates on a test host range of 16 species. Weeds found to be naturally infected were (number of plants infected/number of plants indexed - 1972 and 1973): *Asclepias syriaca* (3/113), *Barbarea vulgaris*+ (13/52 - 1973 only), *Capsella bursa-pastoris*+ (1/12), *Cerastium arvense** (6/42 - 1973 only), *Echinocystis lobata* (11/42), *Eupatorium dubium** (1/8 - 1973 only), *Galinsoga parviflora*+ (4/10 - 1973 only), *Phytolacca americana* (1/35), *Rorippa islandica** (21/156 - 1973 only), *Solanum dulcamara** (3/41), *Stellaria* sp. (4/19) and *Verbascum thapsus** (3/22 - 1973 only). The occurrence of broad bean wilt virus (BBWV) in the plants sampled was noted. The identity of representative isolates of CMV and BBWV was confirmed additionally by studies involving serology and electron microscopy. Lettuce mosaic virus was not recovered from any of the weed samples tested.

Considerable losses occur annually in late season lettuce (*Lactuca sativa* L.) grown in Oswego County, New York, because of cucumber mosaic virus (CMV), lettuce mosaic virus (LMV), or a combination of both (1, 3). A third virus, broad bean wilt (BBWV), also has been detected at low levels in lettuce grown in the area (1). Both CMV and LMV cause similar symptoms in lettuce: systemic chlorotic mottling, stunting, and improper heading (4). Cucumber mosaic virus caused heavy commercial losses in celery (*Apium graveolens* L. var. *dulce* Pers.) grown in one field in Orange County in 1971 (3). The losses resulted from the development of brown sunken areas on the petioles of celery in transit. Twenty of twenty-two plants collected from this field were infected with CMV (3).

Cucumber mosaic virus has a wide host range. Price (16) lists 191 plant species in 40 families susceptible to CMV. Weeds have been reported to carry CMV through the winter in infected plant parts. Detailed indexing of weeds near commercial lettuce and celery fields for CMV in New York previously has not been accomplished. Three plants naturally infected with CMV in New York are *Berberis thunbergii* DC., *Sonchus asper* (L.) Hill, and *Asclepias syriaca* L. (1, 24). The latter two were collected near lettuce fields in Oswego County (1). *Sonchus asper* and *Amaranthus retroflexus* L. were naturally infected with BBWV (1).

The occurrence of weeds listed as important sources of CMV differs considerably for each location. Only by indexing weeds growing near lettuce and celery plantings is it possible to determine the natural weed hosts of CMV which occur locally. This knowledge will be valuable for epidemiological studies of CMV and may be useful in future control programs.

MATERIALS AND METHODS

During the summers of 1972-73 weeds were collected from within and around lettuce and celery fields with histories of CMV. Samples were collected from six lettuce farms in Oswego County and one celery field in Orange County, placed in an ice-cooled styrofoam cooler and transported to Ithaca. The samples were stored at 4.4 C (40 F) until indexing. Because excessive samples were collected in 1972 (more than could be indexed as fresh material) leaves of extra samples were freeze-dried on a VirTis automatic freeze-dryer (Model 10-010) and stored in glass vials in a freezer for later indexing. In 1973, a technique of vacuum-desiccating leaves was used (2). When CMV was detected in a sample, many specimens of that plant species then were collected from the area under investigation to increase the accuracy of measuring the incidence of the virus.

A mechanical inoculation procedure was used throughout the study. Infected leaf tissue was crushed in tap water with a sterilized mortar and pestle. A sterilized gauze pad was dipped into the crude sap and rubbed gently over plant leaves previously dusted with 22-μm

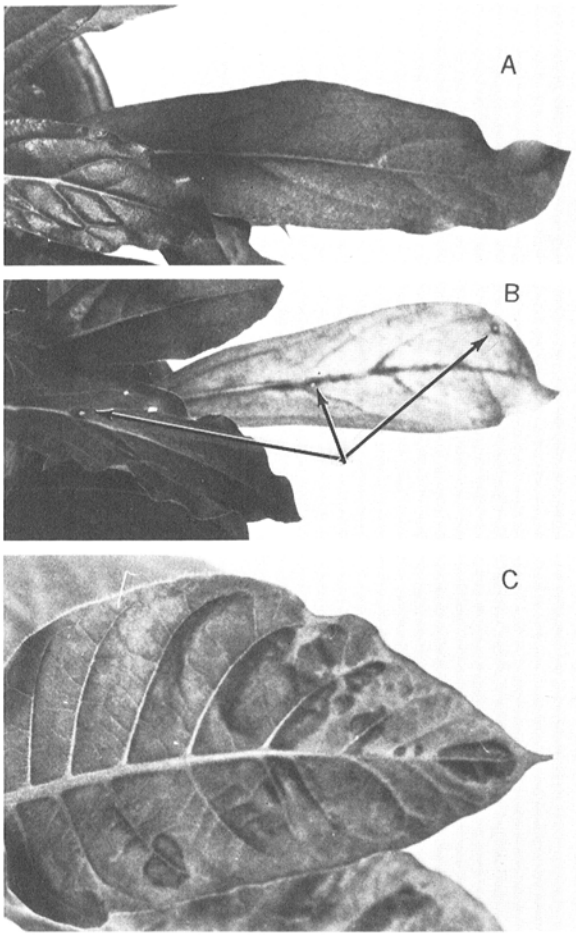

Fig. 1-(A to C). Reactions of *Gomphrena globosa* and *Nicotiana tabacum* 'Samsun NN' to infection by cucumber mosaic virus (CMV): **A)** healthy leaves of *G. globosa*; **B)** chlorosis on the inoculated leaf and necrotic areas with red borders (arrows) on both inoculated and uninoculated leaves of *G. globosa;* and **C)** systemic mosaic symptoms on a leaf of *N. tabacum*.

(600-mesh) Carborundum (The Carborundum Co., Niagara Falls, New York). Rubbed leaves were washed with a stream of tap water. Plants were placed in the greenhouse for about 3 weeks and observed for symptom development. Temperatures in the greenhouse generally were between 18.3 C and 23.9 C, but reached 15.5 C and 37.8 C. Controls consisted of one representative of each plant species used in the treatment, each mechanically rubbed with a gauze pad dipped into tap water.

Routine testing was accomplished by rubbing one plant each of *Gomphrena globosa* L. and *Nicotiana tabacum* L. 'Samsun NN' (tobacco) with crude juice of each sample (Fig. 1). When a reaction was observed on either or both of these plants, the symptomatic leaves were used as a source of inoculum in a host range test consisting of eight species for differentiating CMV and LMV (Table 1, footnote c). Isolates tested were classified as CMV, LMV, or unknown. A number of representative isolates of CMV and LMV from the tests were maintained in one plant each of *G. globosa* and tobacco. These isolates were tested on a host range of 16 species (Table 1). The eight differential hosts originally utilized also were included in this expanded host range.

Other tests for confirming the identification of CMV isolates involved the determination of properties in vitro, purification and serology (17, 18). A 1% bacto-agar medium with six member wells surrounding a central antiserum depot was utilized for serological tests. Tobacco was used as a source plant for all tests. The virus was increased by mechanically inoculating additional tobacco plants and harvesting the inoculated leaves 3 days later (21).

Broad bean wilt virus was identified on the basis of host range, serology, and electron microscopy. Serological tests were performed as described except that 1% agarose gel (Sigma Chemicals, St. Louis) was the medium and source plants were *Vicia faba* L. (fava bean) and *Pisum sativum* L. 'Wando' (pea). Electron microscopy consisted of studying crude juice preparations with a Philips 200 electron microscope. A drop of crude juice from infected *G. globosa* was placed on a formvar and carbon-coated grid for 30 seconds, removed, and the grid was stained with 2% phosphotungstic acid (pH 6.85) for 5 seconds.

RESULTS

Virus identification.—Reactions characteristic for the isolates tested and regarded as diagnostic for CMV were: small, red-brown necrotic spots on *Vigna sinensis* (L.) Engl. 'Early Ramshorn'; chlorotic areas on inoculated and systemically infected leaves of *Cucumis sativus* L. 'Marketer'; systemic vein clearing followed by chlorotic mottling or mosaic on tobacco; systemic vein clearing followed by mosaic and often stunting, distortion, and severe rugosity on *N. glutinosa* L.; chlorotic areas followed by necrosis on inoculated leaves of *Chenopodium quinoa* Willd. (Table 1).

Thermal inactivation of the CMV isolates tested was between 65 and 75 C. The dilution end point was between 1:10,000 and 1:100,000. Inactivation in vitro was between 4 and 6 days.

Three typical CMV isolates reacted with CMV antiserum (ATCC AS-39) in six double-diffusion Ouchterlony plates. Crude tobacco juice only was used in five of the plates, but in the sixth plate both crude and partially purified preparations were tested against the antiserum (Fig. 2). Since difficulty had been experienced in earlier tests in obtaining a precipitin reaction with the partially purified preparations, sodium dodecyl sulfate (SDS) was added to the two wells of this plate after the preparations had diffused into the agar. This was accomplished in hopes of stripping the protein off of the virion and thus making it more available to react with the antiserum. At the time of the test, it was not known that SDS would react nonspecifically with virus antisera (12), and since proper SDS controls were not used, we are not prepared to draw conclusions concerning the bands associated with the partially purified preparations. However, based on the reactions associated with the crude juice preparations, because there was no specific reactions associated with the control wells in any of the

TABLE 1. Differential host range for identifying isolates of cucumber mosaic virus (CMV), lettuce mosaic virus (LMV), and broad bean wilt virus (BBWV)

Host plant	Symptoms induced by each virus[a,b]		
	CMV	LMV	BBWV
Apium graveolens L. var. *dulce* Pers. 'Florida 683' Celery	--;Pos	--;Neg	--;NT
Beta vulgaris L.[c] Sugar Beet	I;L,X,C	--;Neg	--;NT
Brassica rapa L. 'Purple Top White Globe' Turnip	--;Neg	--;Neg	--;NT
Capsicum annuum L. 'Early Calwonder' Pepper	S;C,(D), St	--;Neg	--;NT
Chenopodium amaranticolor Coste & Reyn. Goosefoot	I;L,O,C	I;L,X,C S;X,C,(D)	I;L,X,C S;D,C,N
C. quinoa Willd.[c] Lamb's Quarters	I;L,X,C,N	I;L,X,C S;X,C,(D)	I;L,X,C S;D,C,N
Cucumis sativus L. var. 'Marketer'[c] Cucumber	I;L,X,C S;X,C,St	--;Neg	--;NT
Datura stramonium L.[c] Jimson Weed	I;L,X,C (S;m)	--;Neg	I;O,N
Gomphrena globosa L.[c] Globe Amaranth	I;L,O,N(red border),X,C S;L,O,N,(D),St	I;L,O,R	I;L,X,C S;D,C,N
Lactuca sativa L. 'Minetto' Lettuce	I;C S;C,D,St or --;Pos	I;C S;C,D,St or --;Pos	--;NT
Nicotiana glutinosa L.[c]	(I;L,X,C) S;M or m,St	--;Neg	--;NT
N. tabacum L. 'Samsun NN'[c] Tobacco	(I;L,X,C) S;M or m,St	--;Neg	--;Pos
Phaseolus vulgaris L. 'Bountiful' Bean	(I;L,O,N)	--;Neg	--;NT
Pisum sativum L. 'Wando' Pea	I;L,N	S;m	S;M
Vicia faba L. Broad Bean	(I;L,O,R)	--;Neg	(I;N) S;m,N
Vigna sinensis (L.) Engl. 'Early Ramshorn'[c] Cowpea	I;L,O,R	--;Neg	I;L,X,C S;C,m

[a]Symbol to the left of semicolon indicates leaf on which symptoms appeared. Symbol to the right of semicolon describes the reaction observed. Absence of reaction description for either inoculated or uninoculated leaf means no reaction was observed on those leaves of the associated species. Uninoculated leaves of plants showing no reaction were tested for symptomless infection by inoculating *Chenopodium quinoa* test plants. Neg = index of uninoculated leaf on *C. quinoa* was negative (no symptomless infection). Pos = index of uninoculated leaf on *C. quinoa* was positive (symptomless infection). Enclosure of symbol(s) in parentheses ( ) means that the reaction did not occur regularly.

[b]Symbols: - - = none apparent, C = chlorosis or chlorotic, D = distortion, I = inoculated leaf, L = localized reaction, M = mosaic symptoms, m = mottling, N = necrosis or necrotic, NT = not tested, O = discrete lesion margin, R = red or red-brown, S = systemic (reaction on uninoculated leaf), St = stunting, X = diffuse lesion margin.

[c]Plant species in the eight plant host range.

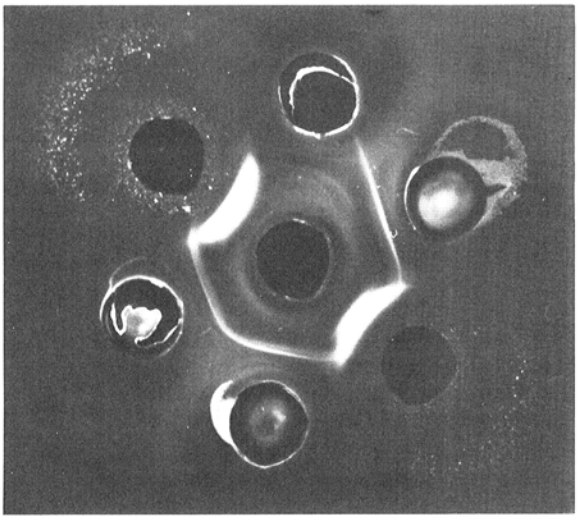

Fig. 2. Immunodiffusion plate with precipitin reactions between isolates of cucumber mosaic virus (CMV) and CMV antiserum (ATCC AS-39). The center well was filled with CMV antiserum. Peripheral wells (clockwise starting from the top well) were filled with: crude juice from healthy tobacco (*Nicotiana tabacum* 'Samsun NN'), crude juice from tobacco infected with CMV isolate C 72-3, a partially purified preparation of CMV isolate C 72-3, crude juice from tobacco infected with CMV isolate Fos 3-1c, crude juice from tobacco infected with CMV isolate F-8, and a partially purified preparation of CMV isolate F-8.

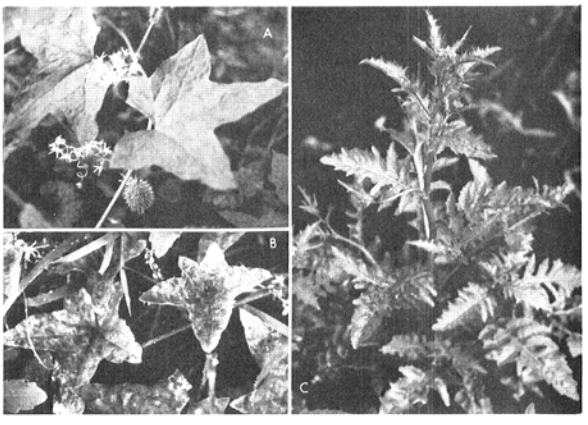

Fig. 3-(A to C). *Echinocystis lobata* and *Rorippa islandica,* two weed species naturally infected with cucumber mosaic virus (CMV) in New York State. **A)** leaf, flower, and fruit of healthy *E. lobata*; **B)** chlorotic mottle of CMV-infected leaves of *E. lobata*; and **C)** *R. islandica,* a symptomless host of CMV.

plates (filled with crude juice from healthy tobacco), and since there were no reactions associated with crude juice preparations from BBWV-infected plant tissues and the CMV antiserum, we feel that the three isolates tested are CMV.

Testing.—Specimens of 12 of the 66 weed species (2) collected during the summers of 1972 and 1973 were infected with CMV (Tables 2 and 3). *Echinocystis lobata* (Michx.) T. & G., *A. syriaca* and *Stellaria* sp. were infected in samples collected both summers.

Weeds collected both in Oswego and Orange Counties and tested for CMV were *Barbarea vulgaris* R. Br., *Rorippa islandica* (Oeder) Borbas (Fig. 3-C), *Stellaria* sp. and *Phytolacca americana* L. Cucumber mosaic virus was detected in *B. vulgaris* and *R. islandica* from both counties. Infected *P. americana* and *Cerastium arvense* L. were collected only in Orange County. *Stellaria* sp. was infected only in Oswego County.

Cucumber mosaic virus was detected in one symptomless *P. americana* sample collected in Orange County on 30 June 1973. Three other samples were collected later from the same plant in an attempt to confirm the earlier finding, but CMV was not recovered. In Oswego County, *P. americana* was found in abundance in several locations. Most mature plants exhibited characteristic systemic mosaic symptoms of dark and light patches on the leaves. Young plants were asymptomatic. Cucumber mosaic virus was not recovered from any samples tested.

Cerastium arvense commonly grows in large masses on the ditchbanks surrounding celery fields in Orange County. The samples infected earliest in the season were collected on 23 May 1973. Of 42 samples collected and tested throughout the summer, 14% were infected with CMV (Table 3).

Stellaria sp. was collected in both counties. Cucumber mosaic virus was recovered only from samples collected in Oswego County. These plants were eradicated by June preventing further sampling studies.

Echinocystis lobata was found on only one farm in Oswego County. Plants were observed and tested from the time of seedling emergence until fruit set. Symptoms of systemic chlorotic spotting were not observed and CMV was not identified in these plants until early August when symptoms were visible. At this time the plants were quite large. By mid-August nearly 100% of the vines had characteristic symptoms of CMV infection. Cucumber mosaic virus was recovered from all such vines (Fig. 3-B).

Solanum dulcamara L., *Capsella bursa-pastoris* (L.) Medic., *Eupatorium dubium* Willd., and *Verbascum thapsus* L. were collected only in Oswego County and were not common near lettuce fields. Incidence of CMV was 7, 8, 12.5, and 14 percent, respectively, of samples collected (Table 3). Symptoms were not apparent on any of these species.

Asclepias syriaca was very common in Oswego County, but only 3% of the samples collected were infected with CMV (Tables 2 and 3). All of the samples infected with CMV were collected during September of both years, the time when lettuce samples also were most commonly infected with CMV. No symptoms were observed which could be associated with CMV infection.

Cucumber mosaic virus was recovered from one *Brassica rapa* L. sample collected from a small planting on one lettuce farm in Oswego County. Nearly all the plants in the field were mottled and mildly distorted. Attempts to inoculate *B. rapa* 'Purple Top White Globe' with this or any other CMV isolate in the greenhouse were unsuccessful (Table 3).

TABLE 2. Plant species from two counties in New York naturally infected with cucumber mosaic virus in 1972[a]

Scientific and common name	County		Total
	Orange	Oswego	
Stellaria sp. Chickweed	1/5	. . .[b]	1/5
Asclepias syriaca L. Milkweed	0/2	1/14	1/16
Echinocystis lobata (Michx.) T. & G. Wild Cucumber	. . .	3/6	3/6
Phytolacca americana L. Pokeweed	. . .	0/2	0/2
Solanum dulcamara L. Nightshade	. . .	0/1	0/1
Capsella bursa-pastoris (L.) Medic. Shepherd's Purse	. . .	0/1	0/1

[a]Numbers of samples infected over the total number indexed.
[b]Indicates none collected.

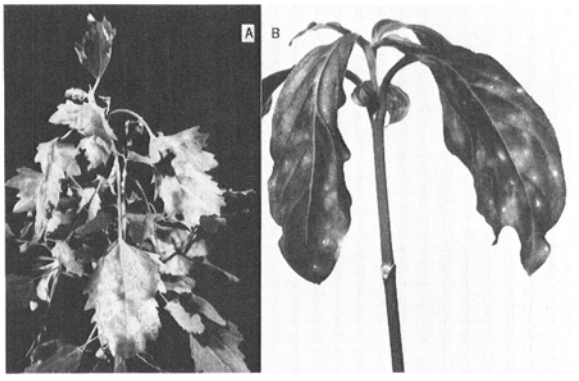

Fig. 4-(A, B). Reactions of *Gomphrena globosa* and *Chenopodium quinoa* to infection by broad bean wilt virus (BBWV): **A)** epinasty and chlorosis of younger leaves and apical necrosis of uninoculated leaves of *C. quinoa*; and **B)** chlorotic and necrotic areas and epinasty of inoculated leaves of *G. globosa*.

Galinsoga parviflora Cav. samples collected by R. Provvidenti and R. G. Grogan were infected with LMV in their tests (R. Provvidenti, *personal communication*). Four of 10 plants collected from the area of their sampling were infected with CMV in the present study. One of these plants exhibited systemic vein clearing and some distortion of the youngest leaves (Table 3).

Lettuce mosaic virus never was detected in any weed species tested in the present study. Broad bean wilt virus was detected in one motherwort plant (*Leonurus cardiaca* L.) collected in Oswego County. Diagnostic host plant reactions included indefinite chlorotic areas followed by a dramatic systemic chlorosis on *G. globosa* (Fig. 4-B). Indefinite chlorotic areas on inoculated leaves and apical necrosis occurred in *C. quinoa* (Fig. 4-A). Systemic chlorotic mottling followed by wilting occurred on both *V. faba* and *P. sativum*. Systemic mottling of the trifoliates occurred on *V. sinensis*. In serological studies a precipitin reaction was observed between the well filled with antiserum of BBWV serotype II (ATCC AS-92) and wells filled with crude juice from infected *V. faba*. No reaction was observed associated with the healthy *V. faba* juice or in plates in which BBWV serotype I antiserum (22) (ATCC AS-90) was used. Polyhedral particles about 27 nm in diameter were associated with crude preparations of infected *G. globosa* but were not seen in preparations from healthy *G. globosa* juice.

DISCUSSION

We have demonstrated that certain ubiquitous weeds growing near lettuce and celery fields in New York are commonly infected with CMV. Eight of the 12 species infected have not been reported as hosts of CMV before in the United States. Other weeds that were given special attention because of earlier publications seemed to be unimportant as sources of the virus in our findings. This is the first report of infection of *C. arvense*, *E. dubium*, *R. islandica*, *S. dulcamara*, and *V. thapsus* by CMV. *Barbarea vulgaris*, *C. bursa-pastoris* and *G. parviflora* are reported to be infected with CMV for the first time in the United States.

Three of the above species (*B. vulgaris*, *C. arvense*, and *R. islandica*) are considered as likely overwintering hosts of CMV since they appear in the field very early, were commonly infected with the virus where studies were made, and constituted a significant proportion of the flora near the fields. Rosettes of *B. vulgaris* and green plants of *C. arvense* have been observed through the winter, but *R. islandica*, a taprooted annual or biennial (11), has not been seen with above-ground parts persisting through the winter. We feel that this plant may be able to

TABLE 3. Plant species from two counties naturally infected with cucumber mosaic virus in New York State in 1973[a]

Scientific and common name	County		Total
	Orange	Oswego	
Barbarea vulgaris R. Br. Yellow Rocket	3/14	10/38	13/52
Rorippa islandica (Oeder) Borbas Yellow Cress	7/78	14/78	21/156
Stellaria sp. Chickweed	0/4	3/10	3/14
Cerastium arvense L. Chickweed	6/42	. . .[c]	6/42
Phytolacca americana L. Pokeweed	1/4[b]	0/29	1/33
Asclepias syriaca L. Milkweed	. . .	2/97	2/97
Solanum dulcamara L. Nightshade	. . .	3/40	3/40
Capsella bursa-pastoris (L.) Medic. Shepherd's Purse	0/5	1/6	1/11
Echinocystis lobata (Michx.) T. & G. Wild Cucumber	. . .	8/36	8/36
Verbascum thapsus L. Mullein	. . .	3/22	3/22
Galinsoga parviflora Cav. Galinsoga	. . .	4/10	4/10
Brassica rapa L. Turnip	. . .	1/1	1/1
Eupatorium dubium Willd. Spotted Joe Pye Weed	. . .	1/8	1/8

[a]Number of samples infected over the total number indexed.
[b]All samples were collected from the same plant.
[c]Indicates none collected.

survive the winter because of the large taproot. *Rorippa islandica* appears before the crop is very old and may be important as a primary source of CMV if not as an overwintering host.

We were particularly interested in *E. lobata, A. syriaca,* and *P. americana* because of earlier published reports of infection by CMV (6, 8). None of these species seems to be important as a source of CMV in New York except possibly *E. lobata*. The fact that *E. lobata* never was symptomatic until early August and the CMV infection was only associated with symptomatic plants indicates that *E. lobata* does not overwinter CMV in infected seed and that it is not likely to be an important source of the virus. It may be a significant secondary source since most of these large vines are infected by mid-August. It was observed only on one farm in Oswego County and does not seem to be of major importance in CMV epidemiology. *Asclepias syriaca,* ubiquitous in Oswego County, was not infected until September and symptoms similar to those reported by Doolittle and Walker (7) were never observed. These findings agree with the report by Faan and Johnson (10) who found that CMV was easily recoverable from *A. syriaca*.

Cucumber mosaic virus recovery from *P. americana* may have been substantially reduced due to inhibitors known to exist in this species (5), but another virus, pokeweed mosaic, has been described in pokeweed samples from Virginia, Kentucky, and Connecticut by Diachun (5). Diachun never detected CMV from those samples and the symptoms he listed for CMV infection of pokeweed were not seen in pokeweed observed in the present study. It may be that the symptomatic plants tested were infected with CMV.

Plant species previously described as naturally infected with CMV but not found to be infected in the present survey are: *A. retroflexus* L. (20), *Ambrosia artemisiifolia*

L. (23), *Brassica napus* L. (15), *Daucus carota* L. (14), *L. cardiaca* L. (10), *Lychnis alba* Mill. (10), *Portulaca oleracea* L. (15), *Rubus* sp. (raspberry) (13, 14), *Thlaspi arvense* L. (19), *Trifolium hybridium* L. (15), and *Valeriana officinalis* L. (10).

The results described herein have added significantly to our understanding of the ecology of CMV. *Rorippa islandica* seems certainly to be involved as a source of the virus in both counties in New York, whereas *C. arvense* appears to be only in Orange County. We are unsure of the role which *B. vulgaris* plays in this system, since it appears so early and goes to seed by mid-June. This is at least one month before the suspected aphid vector populations reach their peak. It is possible that early in the season there is low-level aphid activity of which we are unaware that may be spreading CMV from *B. vulgaris* to another host. This host may then serve as a source of virus for spread into the lettuce at a later time. We have, however, no indication that CMV is present in any of the fields observed before August, so the idea of early aphid spread is not supported in this respect.

It is unlikely that any one weed is a keystone which when eliminated will result in the control of a naturally occurring virus in the field (9). Significant reduction in the incidence of CMV in cucumber fields has been reported after all known susceptible perennial weeds growing within 50 to 75 yards of the fields were eradicated (8). However, the effectiveness of weed eradication as a control measure has been questioned by Faan and Johnson (10) after they observed a low incidence of CMV occurring in the susceptible weeds listed by Doolittle and Walker (8) even though the incidence of CMV in the cucumber plantings was high. Only well controlled field studies on the dynamics of CMV spread will resolve these problems.

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