Three Filamentous Viruses Isolated from Sweet Potato in Japan

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Abstract

Three filamentous viruses were isolated from sweet potato by sap inoculation. The M-isolate infected *Ipomoea* spp., *Nicotiana tabacum*, *N. benthamiana*, *Datura stramonium*, *Chenopodium quinoa*, *C. amaranticolor*. The Mo-isolate infected *Ipomoea* spp., *C. quinoa* and *C. amaranticolor*. The C-isolate infected only *Ipomoea* spp. The infectivities of the M-, Mo- and C-isolates were lost at dilutions of 1:1,000–1:10,000, 1:1,000–1:10,000 and 1:100–1:1,000, respectively, or after storage for one day at 20°C. The thermal inactivation points were 50–60°C, 60–70°C and 70–80°C, respectively. Virus particles of the M- and Mo-isolates were 750–810 nm and 850–880 nm long, respectively. The C-isolate was 710–760 nm and 1,430–1,510 nm long. The particle diameter of all isolates was 13 nm. The M-isolate was easily transmitted by *Myzus persicae* but Mo- and C-isolates were not. The serological relationship between the M-isolate and sweet potato latent virus (SPLV) occurring in Taiwan was observed by serologically specific electron microscopy using protein A gold (SSEM-PAG). The Mo-isolate strongly reacted with antisera against sweet potato feathery mottle virus-russet crack strain (SPFMV-RC) found in the United States and SPFMV in Japan. No close serological relationship was found among three isolates. These results suggested that M- and Mo-isolates are strains of SPLV and SPFMV, respectively, and the C-isolate is a new virus, which we named sweet potato symptomless virus (SPSV).

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Key words: sweet potato latent virus, sweet potato feathery mottle virus, sweet potato symptomless virus.

INTRODUCTION

Four viruses, sweet potato feathery mottle virus (SPFMV)³⁾, sweet potato shukuyo mosaic virus (SPSMV)³⁾, sweet potato leaf curl virus (SPLCV)⁸⁾ and cucumber mosaic virus (CMV)³⁾, have been reported in Japanese sweet potato. SPFMV, widely distributed throughout sweet potato growing areas in Japan, causes various symptoms on the lower leaves of sweet potato, such as chlorotic spots, some with purple borders, and chlorotic vein banding. SPLCV, transmitted by the whitefly *Bemisia tabaci*, causes characteristic curling on the leaves of sprouts, but this curling decreases with an increase in temperature and disappears by the last nursery stage.

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The disease is widespread in southern Kyushu. SPSMV occurred at one region of Yamanashi Prefecture in 1957, transmitted by the aphid *Myzus persicae*, and the crop suffered heavy damage. However, the disease was stamped out by thorough elimination of the affected crops. The causal virus of the disease is now considered to be a virulent strain of SPFMV. CMV has been occasionally isolated from SPFMV-affected plants, but its effect on sweet potato has not been clarified.

In 1980, an apparently hitherto undescribed disease of sweet potato (cv. Kokei No. 14) in Japan, which is very similar to the russet crack disease in the United States, was reported in Kagoshima Prefecture⁹). The fleshy roots became affected by darkened or brown lesions composed of fine longitudinal cracks which extended in transverse bands of varying width on the surface. Severely affected roots were covered entirely with cracks, although the inner flesh of the roots seemed unaffected. The disease is called "Obijo-sohi" in Japanese. The causal agent is considered to be a virus because the disease can be eliminated by meristem tip-culture, and the occurrence of the disease in meristem tip-cultured sweet potato is closely associated with filamentous virus.

In this study, we tried to isolate the causal agent of the disease by mechanical inoculation from sweet potato to *Ipomoea nil*. We describe the three different filamentous viruses which were isolated.

MATERIALS AND METHODS

Virus source and inoculation. Lower leaves of sweet potato (cv. Kotobuki No. 1) affected with 'Obijo-sohi' disease served as the initial virus source. The fleshy roots which exhibited the typical symptoms were kindly supplied by Mr. R. Nagata. The leaves were macerated with 0.1 M phosphate buffer (pH 8.0) containing 0.1% thioglycolic acid and inoculated to primary leaves of *I. nil* (Scarlet O'Hara) plants at primary leaf stage. The inoculated plants were kept in a greenhouse or growth chamber controlled at 22°C.

Properties of virus isolates in sap. The properties of the virus isolates in the sap of *I. nil* were determined using preparations of systemically infected leaves macerated with 0.1 M phosphate buffer (pH 8.0) containing 0.1% thioglycolic acid in a mortar and pestle. The sap was collected by squeezing through cheesecloth. The inoculated *I. nil* plants were kept in a greenhouse.

Virus particle length distribution. Virus particle length was measured by examin-

1. Float carbon-coated grids on drops of antiserum diluted 1:1,000 with 0.05 M Tris buffer (pH 7.2) for 30 min.
2. Wash grids with distilled water.
3. Float grids for 1 hr on extracts made by grinding 1 g of infected *I. nil* leaves with a mortar and pestle with 30 ml of 0.02 M phosphate-buffered saline, pH 7.4, containing 0.05% Tween 20.
4. Wash grids with distilled water.
5. Float grids for 20 min on drops of antiserum diluted 1:1,000 with 0.02 M Tris-buffered saline (pH 7.5) containing 1% bovine serum albumin (BSA-TBS).
6. Wash grids with 0.02 M Tris-buffered saline containing 0.05% Tween 20 (TTBS).
7. Float grids for 10 min on drops of protein A gold (Protein A 10, Janssen Inc.) diluted 1:25 with BSA-TBS.
8. Wash grids with TTBS.
9. Wash grids with distilled water.
10. Stain grids with 2% PTA.
11. Examine the samples with an electron microscope.

Fig. 1. Procedure for serologically specific electron microscopy using protein A gold (SSEM-PAG).

ing sap preparations of fresh leaves infected with each virus isolate stained with 2% phosphotungstic acid (pH 7.0). Electron micrographs of each virus isolate and tobacco mosaic virus (TMV) were simultaneously taken with a Hitachi H-500 electron microscope under 10,000 magnification. Measurements were made by comparing particle size with the peak of the TMV particle length distribution (300 nm).

Purification. All the isolates were purified from *I. nil* leaves according to the method of Cali and Moyer¹⁾, with the following modifications. Cesium chloride, 1.85 g, was added to 5 ml of the partially purified preparation which was then centrifuged for 4 hr at 50,000 rpm (Hitachi vertical rotor RP65VF). After centrifugation, the band containing virus particles was collected and dialyzed against resuspension buffer (0.05 M borate buffer, pH 8.0 containing 0.5 M urea and 1% Triton X-100).

Serology. Purified preparations were used to produce antisera. The rabbits were intramuscularly injected with purified preparations emulsified with an equal amount of complete Freund's adjuvant three times at 20-day intervals. SSEM-PAG (serologically specific electron microscopy using protein A gold) was performed as described in Fig. 1.

RESULTS

Establishment of three virus isolates in I. nil

Ipomoea nil inoculated with sap of the lower leaves of sweet potato (cv. Kotobuki No. 1) with Obijo-sohi disease developed various symptoms such as vein clearing, mottling, mosaic, slight and severe curling, chlorotic vein banding and yellow netting on the first and second true leaves. Chlorotic spots were observed on the upper leaves when the plants matured. As the symptoms of individual plants were varied, the plants showing typical symptoms were used as inocula and inoculated to *I. nil* again.

The plants inoculated with the sap of leaves showing slight curling developed slight vein clearing and curling followed by necrosis of the leaf vein, petiole and stem as in the original plants under 22°C (Fig. 2). The symptoms were established by successive sap inoculations and referred to as the C-isolate.

Inoculation of the sap of plants showing severe curling caused three types of symptoms, slight curling, severe curling and mottling on the first true leaf of *I. nil*. Slight curling was caused by the C-isolate. *I. nil* with mottling consistently developed vein clearing about ten days after inoculation followed by obscure mottling and water-soaked vein banding. Moreover, chlorotic spots were observed on the upper leaves of the plants which had been moved to the greenhouse. This isolate was referred to as the Mo-isolate.

Fig. 2. Curling symptom on *Ipomoea nil* (Scarlet O'Hara) infected with C-isolate.

In the greenhouse, *I. nil* developed vein clearing 5–6 days after inoculation with the sap of leaves showing mosaic or mottle markings. As soon as the vein clearing symptom appeared on the first true leaf, inoculation was done using this leaf as the inoculum. The plants developed vein clearing, followed by mosaic marking on the first and second true leaves. The mosaic symptom was different from that of the Mo-isolate (Fig. 3), and became a characteristic pattern along the vein (Fig. 4). This isolate was referred to as the M-isolate.

Particle length distribution

Electron micrographs of negatively stained preparations of all isolates revealed long, flexuous rods. No similar particles were found in the preparations made from healthy plants. Macerating a piece of leaf with one or two drops of 2% PTA by mortar and pestle yielded more particles than leaf-dip preparations. Measurements of long, flexuous particles of the M-isolate indicated a normal length of 750–810 nm (Fig. 5-a). The normal length of the Mo-isolate was 850–880 nm (Fig. 5-b). The C-isolate preparations contained extremely long flexuous rods and showed two particle length distributions of 710–760 nm and 1,430–1,510 nm (Fig. 5-c). Long particles did not have the cross banding observed with closteroviruses. The diameter of all isolates was about 13 nm.

Host range

Herbaceous plants representing 30 species from 10 families were mechanically inoculated with M-, Mo- and C-isolates. After 20 days, the inoculated as well as upper leaves were inoculated to *I. nil* in order to check latent infection. The results are shown in Table 1. The host range of the C-isolate was limited to *Ipomoea* spp. The Mo-isolate infected the *Ipomoea* species as well as *C. quinoa* and *C. amaranticolor*, although the chlorotic spots on the latter were often very obscure. The M-isolate had a wider host range, some *Nicotiana* species, *Datura stramonium*, *C. amaranticolor* and *C. quinoa*, besides *Ipomoea* species. *N. benthamiana* infected with M-isolate developed clear characteristic mosaic symptoms on the upper leaves, and *D. stramonium* also developed chlorotic spots on the inoculated leaves. All three isolates infected some *Ipomoea* species, with plants infected with the M-isolate showing clearer symptoms. Although *I. setosa* inoculated with C-isolate by sap inoculation did not develop any symptoms, it showed necrotic spots on the lower leaves followed by necrosis when inoculated by grafting.

Stability in sap of *I. nil*

The infectivities of M-, Mo- and C-isolates were lost at dilution between 1:1,000–1:10,000, 1:1,000–1:10,000 and 1:100–1:1,000, respectively, and after storage for one day at 20°C. The

Fig. 3. Mosaic symptom on *I. nil* infected with M-isolate.

Fig. 4. Characteristic chlorosis on upper leaf of *I. nil* infected with M-isolate.

Fig. 5. Particle length distribution of three isolates in preparation from fresh leaves of *I. nil*. M-isolate (a), Mo-isolate (b), C-isolate (c).

Table 1. Host range of three viruses isolated from sweet potato ^{a)}

Plant	M	Mo	C
<i>Nicotiana tabacum</i> (White Burley)	—	—	—
(Samsun)	—	—	—
(Havana)	1/— ^{b)}	—	—
(Xanthi)	1/—	—	—
<i>N. benthamiana</i>	M	—	—
<i>N. glutinosa</i>	—	—	—
<i>N. debney</i>	—	—	—
<i>Datura stramonium</i>	CS/—	—	—
<i>Physalis floridana</i>	—	—	—
<i>Lycopersicon esculentum</i> (Kyoryoku Beiju)	—	—	—
<i>Capsicum annuum</i> (New Face)	—	—	—
<i>Spinacia oleracea</i>	—	—	—
<i>Chenopodium quinoa</i>	CS/—	CS/—	—
<i>C. amaranticolor</i>	CS/—	CS/—	—
<i>Glycine max</i> (Norin No. 4)	—	—	—
<i>Pisum sativum</i> (Kinusaya)	—	—	—
<i>Vicia faba</i> (Sanuki Nagasaya)	—	—	—
<i>Phaseolus vulgaris</i> (Tsurunasi Kintoki)	—	—	—
<i>Vigna sesquipedalis</i> (Kurodane Sanjaku)	—	—	—
<i>Sesamum indicum</i> (Kurogoma)	—	—	—
<i>Zea mays</i>	—	—	—
<i>Tetragonia expansa</i>	—	—	—
<i>Gomphrena globosa</i>	—	—	—
<i>Raphanus sativus</i> (Kuroha mino Wase)	—	—	—
<i>Citrullus lanatus</i> (Zuisyo)	—	—	—
<i>Cucumis sativus</i> (Kinpyo)	—	—	—
<i>Cucurbita maxima</i> (Ebisu)	—	—	—
<i>Ipomoea nil</i> (Scarlet O'Hara)	M	Mo, CS	N/VC, C, N
<i>I. setosa</i>	VC	VC	—
<i>I. purpurea</i>	l	VC	VC, N
<i>I. triloba</i>	VC, Mo, PRS	PRS	l
<i>I. trichocarpa</i>	VC, M, PRS	CS	CS
<i>I. lacunosa</i>	CS, VC, PRS	VC, Mo	VC

a) CS=chlorotic spot; VC=vein clearing; M=mosaic; Mo=mottle; N=necrosis; PRS=purple ring spot; l=latent infection; C=curling; —=no infection.

b) Inoculated leaf/upper leaf.

thermal inactivation points of M-, Mo- and C-isolates lay between 50–60°C, 60–70°C and 70–80°C, respectively.

Transmission by aphids

M-isolate could be transmitted in a nonpersistent manner from *I. nil* to *I. nil* by *Myzus persicae* starved for two hours, but Mo- and C-isolates could not (Table 2).

Purification

When partially purified preparations were subjected to CsCl equilibrium density gradient centrifugation, a faint opalescent band was observed near the bottom of the tube. The electron microscopy observation of preparations recovered from the band in the gradient revealed that the band was composed of many virus particles and a few impurities from host plants. Aggregation of virus particles of M-isolate was observed in preparations stained with PTA (Fig. 6), but not of Mo- and C-isolates (Figs. 7 and 8). When purified preparations of C-, Mo- and M-isolates were inoculated to *I. nil*, high, low and no infectivities were observed, respectively.

Serology

As antigens of Mo-isolate were identical to SPFMV reported by Nakano *et al.* (1984)⁵⁾ in the agar gel immunodiffusion test, antiserum against SPFMV was substituted for it against Mo-isolate. The complement fixation test and SSEM-PAG were done to examine the serological relationship among these three isolates (Table 3). Antisera to SPFMV, M- and C-isolates had homologous titers of 1:640, 1:320 and 1:320, respectively. No close relationship was observed among the three isolates. Although only a slight reaction between the M-isolate and the antiserum against SPFMV was observed in the complement fixation test, this reaction could not be reconfirmed by SSEM-PAG. In SSEM-PAG, many virus particles decorated with γ -globulin molecule and gold particles were observed in homologous combinations but not in heterologous ones.

Many virus particles of M-isolate were trapped and decorated with γ -globulin molecules and gold particles by SSEM-PAG using antiserum against sweet potato latent virus (SPLV) kindly supplied by Dr. Y.H. Hsu, but Mo- and C-isolates were not (Fig. 9). Antiserum against SPFMV-russet crack strain (SPFMV-RC) supplied by Dr. J.W. Moyer, were used to determine the relationship between SPFMV-RC and these three isolates. In SSEM-PAG, only the Mo-isolate was trapped and densely decorated with gold particles (Fig. 10).

Table 2. Transmission of three viruses isolated from sweet potato by *Myzus persicae*^{a)}

Virus isolate	Time of starvation	Time of acquisition feeding	Time of inoculation feeding	Diseased plants
				Inoculated plants
M	0 hr	5–30 sec	5–10 min	0/6
	2.0 hr	5–30 sec	5–10 min	1/7
	2.0 hr	5–30 sec	5–10 min	2/5
	2.0 hr	5–30 sec	5–10 min	3/6
	2.0 hr	5–30 sec	5–10 min	2/8
Mo	2.0 hr	5–30 sec	5–10 min	0/6
	2.0 hr	5–30 sec	5–10 min	0/5
	2.0 hr	5–30 sec	5–10 min	0/9
	2.0 hr	5–30 sec	5–10 min	0/9
	2.5 hr	22 hr	22.5 hr	0/7
C	0 hr	5–30 sec	5–10 min	0/7
	2.0 hr	5–30 sec	5–10 min	0/8
	2.0 hr	5–30 sec	5–10 min	0/6
	2.0 hr	5–30 sec	5–10 min	0/8
	2.0 hr	5–30 sec	5–10 min	0/5

a) Five aphids per one plant (*Ipomoea nil*) were used in each test.

Fig. 6. Purified preparation of M-isolate stained with 2% PTA. Virus particles were aggregated during purification. Bar represents 500 nm.

Fig. 7. Purified preparation of Mo-isolate. Bar represents 500 nm.

Inoculation to sweet potato

Virus-free sweet potato (Kotobuki No. 1) inoculated with each isolate was grown outdoors under cheesecloth, and the fleshy roots were surveyed. None of the plants developed 'Obijoshi' symptoms on the fleshy roots after two crop seasons. However, sweet potato inoculated with the Mo-isolate developed chlorotic spots on the lower leaves and slightly rough skin on the fleshy roots, and the typical red color of the fleshy root slightly faded after the first crop season.

DISCUSSION

All filamentous viruses occurring in Japanese sweet potato have been considered to be SPFMV. However, at least three different ones were isolated from sweet potato in the present

Fig. 8. Purified preparation of C-isolate. Bar represents 500 nm.

Table 3. Serological relationship among three viruses isolated from sweet potato

Antiserum	M	Mo	C	Healthy component
M	320 ^{a)}	0 ^{b)}	0	0
SPFMV ^{c)}	20	640	0	0
C	0	0	320	0

a) Figure is reciprocal of the dilution end point of the antiserum in complement fixation test.

b) 0 means negative reaction of antiserum at dilution 1:10.

c) Nakano *et al.*⁵⁾

Fig. 9. Serological test by SSEM-PAG using antiserum against sweet potato latent virus. Many virus particles of M-isolate were trapped and gold particles were attached to the surface of virus particles decorated with antibody molecules. Bar represents 500 nm.

Fig. 10. Serological test between Mo-isolate and antiserum against sweet potato feathery mottle virus russet crack strain (SPFMV-RC). SSEM-PAG reveals a close relationship between Mo-isolate and SPFMV-RC. Bar represents 500 nm.

study. They were judged as differing from each other from the symptomatology and morphology of the virus particles and serology. The properties of the Mo-isolate are almost the same as those of SPFMV reported previously except that the Mo-isolate is not transmitted by *M. persicae*^{3,6)}. Antigens of the Mo-isolate were identical to those of SPFMV reported by Nakano *et al.*⁵⁾ and strongly reacted with antiserum against SPFMV-RC¹⁾. Moreover, SPFMV reported by Nakano *et al.*⁶⁾ was transmitted by *M. persicae* in a nonpersistent manner (data not shown). Although further study is needed on the transmissibility by aphids, the Mo-isolate is considered to be a strain of SPFMV.

Some properties of the M-isolate coincided with those of SPLV occurring in Taiwan except that the M-isolate is transmitted by *M. persicae* but SPLV is not²⁾. For instance, the M-isolate infected the *Nicotiana* species and *Datura stramonium* besides Convolvulaceae and Chenopodiaceae and reacted with antiserum against SPLV. These results indicate the M-isolate to be a strain of SPLV. This is the first report of SPLV in Japan. We have found that *Calystegia japonica* Choisy with mild mottling and wild morning glory (*I. nil*) with mosaic marking or mottling in Chikugo and Yame City, Fukuoka Prefecture, reacted with antiserum against the M-isolate in SSEM-PAG (data not shown). Therefore, this virus seems to be widely distributed in the Kyushu area.

The present status of research on sweet potato viruses has been reviewed by Moyer and Salazar⁴⁾. Their list of filamentous viruses included SPFMV, sweet potato vein mosaic virus (SPVMV), SPLV, sweet potato mild mottle virus (SPMMV) and sweet potato yellow dwarf viruses (SPYDV). Comparison of the properties of these viruses with those of the C-isolate showed that SPMMV and SPYDV have wider host ranges extending beyond the Convolvulaceae, to which the C-isolate is limited. SPFMV and SPLV are serologically unrelated to the C-isolate. The limitation of the host range of SPVMV to Convolvulaceae is similar to that of the C-isolate. However, symptoms of *I. setosa* and *I. nil* infected with SPVMV differ considerably from those of the C-isolate. The life span of SPVMV *in vitro* is between 10 and 20 days while that of the C-isolate is less than one day. SPVMV has a modal length of 761 nm and is nonpersistently transmitted by *M. persicae*⁷⁾. Thus the C-isolate does not fit the description of any of the viruses. Furthermore, in ultra-thin sections, pinwheel and cylindrical inclusions characteristic of the potyviruses were not observed in the leaf cells of *I. nil* infected with the C-isolate (data not shown). We concluded that the C-isolate is an undescribed virus and named it sweet potato

symptomless virus (SPSV). The virus is often detected in sweet potatoes collected from various areas and therefore seems to be widely distributed in Japanese sweet potatoes. A virus which reacted with antiserum against the C-isolate was found in the Republic of Peru (Nakano, personal communication).

Sweet potato inoculated with M-, Mo- and C-isolates did not develop 'Obijo-sohi' disease on the fleshy roots. Further study is needed to find the causal agents of the disease including study of mixed infection of two or three of these isolates.

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和 文 摘 要

宇杉富雄・中野正明・新海 昭・林 隆治：日本のサツマイモより分離された3種のひも状ウイルスについて

汁液接種によりサツマイモから3種のひも状ウイルスが分離された。M分離株は *Ipomoea* spp., *Nicotiana tabacum*, *Datura stramonium*, *Chenopodium quinoa*, *C. amaranticolor* に、Mo分離株は *Ipomoea* spp., *C. quinoa* および *C. amaranticolor* に、C分離株は *Ipomoea* spp. にのみ感染した。M, Mo および C の希釈限界はそれぞれ、1,000~10,000 倍、1,000~10,000 倍および 100~1,000 倍であり、保存限界は1日以内であった。また、不活化温度はそれぞれ 50~60°C, 60~70°C および 70~80°C であった。M, Mo のウイルス粒子はそれぞれ 750~810 nm, 850~880 nm に、C は 710~760 nm と 1,430~1,510 nm に分布した。ウイルス粒子の幅はいずれもおおよそ 13 nm であった。M は容易にモモアカブラムシによって伝搬されたが、Mo および C は伝搬されなかった。SSEM-PAG により M と台湾で発生する sweet potato latent virus (SPLV) 抗血清との間に、Mo と sweet potato feathery mottle virus russet crack strain (SPFMV-RC) との間に血清関係が認められた。しかし、3分離株の間には血清関係は認められなかった。以上の結果から、M および Mo はそれぞれ SPLV (サツマイモ潜在ウイルス) および SPFMV (サツマイモ斑紋モザイクウイルス) の1系統と考えられた。C はサツマイモでは未記載のウイルスであり、これをサツマイモシンブトムレウイルス (SPSV) と命名したい。