Amazon Lily Mosaic Virus, a New Potyvirus Infecting Amazon Lily (*Eucharis grandiflora*)

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Abstract

A potyvirus, for which the provisional name of Amazon lily mosaic virus (ALMV) is proposed, was isolated from an Amazon lily plant (*Eucharis grandiflora*) with mosaic disease. ALMV which was mechanically transmitted to *E. grandiflora* induced mosaic symptoms on leaves and flower stalks and tiny etched flecks along the veins of flower petals. Necrotic lesions appeared on inoculated leaves of *Chenopodium quinoa* and *C. amaranticolor*, but no systemic infection occurred. ALMV systemically infected *Nicotiana benthamiana* and induced mosaic symptoms. Other 38 plant species in 12 families tested were not infected with ALMV. ALMV was transmitted non-persistently by aphid (*Myzus persicae*). The particle length was about 760 nm. Pinwheel inclusions were observed in the cytoplasm of the mesophyll cells of infected *E. grandiflora* plants. The virus was purified from inoculated leaves of *C. quinoa* by sedimentation with polyethylene glycol 6000 and isopycnic centrifugation in Cs_2SO_4 . The purified virus showed an ultraviolet absorption profile typical of a nucleoprotein with a maximum at 260 nm and a minimum at 246 nm. The A_{260}/A_{280} ratio was 1.32. The virus particles contained a single species of single stranded RNA of M_r 3.32×10^6 , and single polypeptide of M_r 35,000. ALMV was serologically distantly related to *Alstroemeria* mosaic virus, *Hippeastrum* mosaic virus, *Hyacinth* mosaic virus, onion yellow dwarf virus, *Ornithogalum* mosaic virus, potato virus Y, watermelon mosaic virus 2 and zucchini yellow mosaic virus.

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Key words: potyvirus, Amazon lily mosaic virus, Amazon lily, *Eucharis grandiflora*.

INTRODUCTION

The cultivation of Amazon lily (*Eucharis grandiflora*, Amaryllidaceae) for cut flower was markedly promoted in Japan during the past decade. A virus disease occurred soon after the first cultivation of Amazon lily in Okinawa Prefecture. The diseased plants showed extensive mosaic symptoms on leaves and bore severely malformed flowers (Fig. 1).

Brandes¹⁾ found filamentous virus-like particles of 740 nm in length from the plants showing mosaic symptoms by electron-microscopical examinations, and tentatively designated it as *Eucharis* mosaic virus. However, isolation of the virus and its further characterization have not been attempted. Jayasinghe and Dijkstra⁵⁾ designated a filamentous virus appearing in plants of *E. grandiflora* with mosaic disease as *Hippeastrum* mosaic virus (HiMV) based on its serological property, even though they did not succeed in isolating HiMV biologically because of co-existence of another virus with filamentous particle 600 nm in length with HiMV.

Preliminary examinations by immunosorbent electron

microscopy of a *E. grandiflora* plant with mosaic disease collected from Okinawa showed the presence of three types of filamentous virus-like particles. One reacted with the antiserum to HiMV, the second one reacted with the antiserum to *Nerine* latent virus (NeLV), and the third one did not react with either antiserum. The plant with mosaic disease was also found to be infected with cucumber mosaic virus (CMV) by examinations of the simplified double diffusion test¹¹⁾. The third filamentous virus, for which the name Amazon lily mosaic virus (ALMV) was proposed, was isolated and characterized. This paper describes several properties of ALMV and evidence that it is a new member of the potyvirus group.

MATERIALS AND METHODS

Source plants and isolation of virus. *E. grandiflora* plants showing mosaic symptoms were collected from a commercial field in Okinawa Prefecture, and maintained in a greenhouse. Crude sap of the *Eucharis* leaves was inoculated to *Chenopodium quinoa*, and one of the local lesions produced was subjected to single lesion transfer to *C. quinoa* several times. The

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Fig. 1. A *Eucharis grandiflora* plant with mosaic symptoms from which Amazon lily mosaic virus (ALMV) was isolated. Leaves with severe mosaic symptoms (a) and flowers with heavy malformation (b).

isolated virus was propagated in *C. quinoa*.

Host range test. Inoculated leaves of *C. quinoa* 10 days after mechanical inoculation with the virus were homogenized in 0.1 M phosphate buffer (PB) (pH 7.2) containing 0.1% 2-mercaptoethanol (2-ME) and 10 mM sodium ethylenediamine tetraacetic acid (EDTA), and the homogenate was used as the inoculum. Forty-two plant species in 12 families including *E. grandiflora* were mechanically inoculated. Detection of the virus in the inoculated and non-inoculated upper leaves of the test plants was made by back inoculation to *C. quinoa*. As *E. grandiflora* did not produce fertile seeds, virus-free plants of *E. grandiflora* were obtained from symptomless plants propagated through meristem-tip-culture, which were purchased from Gifu Biofarm Ltd. Virus-free plants of *Hippeastrum × hybridum* and *Nerine sarniensis* were grown from seeds.

Aphid-transmission tests. Virus-free aphids (*Myzus persicae*) were starved for 3 hr in Petri dishes and then fed on mechanically infected *Eucharis* plants for 2 min. After the acquisition access, groups of 5 aphids were transferred to each of virus-free *Eucharis* plants for the inoculated access of 30 min.

Virus purification. One hundred grams of inoculated leaves of *C. quinoa* were homogenized in 150 ml of 0.5 M potassium phosphate buffer (KPB) (pH 8.0) containing 0.1% 2-ME, 10 mM EDTA, 40 ml of chloroform, and 40 ml of carbon tetrachloride. The homo-

genate was centrifuged at $8000 \times g$ for 15 min. Polyethylene glycol 6000 (PEG) and Triton X-100 were added to the supernatant to give final concentrations of 5% and 0.5%, respectively. After stirring at 4°C for 1 hr, the mixture was centrifuged at $12000 \times g$ for 20 min. The pellet was resuspended in 0.25 M KPB (pH 8.0) containing 0.1% 2-ME and 0.1% Triton X-100 (resuspending buffer) and centrifuged at $8000 \times g$ for 10 min. After one more cycle of PEG precipitation followed by one cycle of differential centrifugation, the virus was purified by Cs_2SO_4 density gradient centrifugation in resuspending buffer according to the method of Taiwo *et al.*¹²⁾ The virus zone was collected from the gradient, and diluted with two volumes of resuspending buffer. The virus was pelleted by ultracentrifugation and resuspended in 10 mM PB (pH 7.0).

Serology. A rabbit was injected with one mg of purified virus emulsified with Freund's complete adjuvant into the foot-pad and subcutaneously along vertebrae three times at four-week intervals. The blood was collected one week after the last injection. Serological relationships of ALMV with other potyviruses were examined by microprecipitin tests using 200 $\mu\text{g}/\text{ml}$ of purified virus. The antigen and antisera were diluted with 0.1 M Tris-HCl buffer (pH 8.0) containing 0.85% NaCl and 0.05% NaN_3 . The antiserum to HiMV (*Eucharis* isolate) was kindly provided by Dr. J. Dijkstra (Agricultural University, Wageningen, The Netherlands), antisera to HiMV and NeLV by Dr. A.A. Brunt (Littlehampton, England), antisera to *Alstroemeria* mosaic virus (AIMV), onion yellow dwarf virus (OYDV), *Freesia* mosaic virus (FMV) and leek yellow stripe virus (LYSV) by Dr. D.Z. Maat (Research Institute for Plant Protection, Wageningen, The Netherlands), antisera to *Ornithogalum* mosaic virus (OMV), *Hyacinth* mosaic virus (HyMV), *Scilla* mosaic virus (ScMV), and tulip breaking virus (TBV) by Ir. A.F.L.M. Derks (Bulb Research Center, Lisse, The Netherlands). The other antisera used were derived from our own stock.

Electron microscopy. Leaf dip and purified preparations were stained with 2% phosphotungstic acid (pH 7.0). For ultrathin sectioning, small pieces of diseased leaves were fixed with 2.5% glutaraldehyde in 0.1 M sodium phosphate buffer (NaPB) (pH 7.2) for 1 hr, then postfixed with 1% osmium tetroxide in the same buffer for 4 hr. Fixed samples were dehydrated in a series of ethanol and embedded in Spurrs' resin¹⁰⁾. Ultrathin sections were cut with glass knives mounted on an Ultracut N ultratome (Reichert-Nissei). Sections were stained with uranyl acetate and lead citrate and examined with a Hitachi Model H-500 electron microscope.

Nucleic acid. Nucleic acid was extracted from purified virus with water-saturated phenol after incubation with 50 $\mu\text{g}/\text{ml}$ Proteinase K (Boehringer Mannheim) and 1% SDS for 30 min at room temperature. Nucleic acid was dissolved in RNase-free water after ethanol precipitation.

Two hundred nanograms of ALMV nucleic acid were

incubated with 10 $\mu\text{g}/\text{ml}$ of RNase A (Sigma Chemical: DNase activity was eliminated by boiling) or RNase-free DNase I (Worthington Biochemical) for 15 min at 37°C, and electrophoresed in 1% agarose gel using TBE buffer (89 mM Tris-boric acid, 2 mM EDTA, pH 8.3). The gel was stained with 0.5 $\mu\text{g}/\text{ml}$ of ethidium bromide. The digestion with RNase was carried out in 50 mM Tris-HCl buffer (pH 8.0) containing 10 mM EDTA. For the DNase digestion, 33 units of human placental RNase inhibitor (Pharmacia P-L Biochemical) were included in the same buffer without EDTA.

One microgram of ALMV nucleic acid was incubated with 1.8% formaldehyde at 37°C overnight, and the alterations of the profile of UV absorption were analyzed.

To estimate the molecular weight, 1 μg of ALMV nucleic acid denatured with 1 M glyoxal was electrophoresed in 1% agarose gel using 10 mM NaPB (pH 7.0) according to the method of McMaster and Carmichael⁸⁾. Turnip mosaic virus RNA (M_r 3.44×10^6) and tobacco ringspot virus RNA (M_r 2.73×10^6 for RNA-1, 1.34×10^6 for RNA-2) were used as size markers^{3,9)}. The gel was stained with 0.05% toluidine blue O⁹⁾.

Estimation of molecular weight of coat protein.

The purified virus was dissociated with 1% SDS and 1% 2-ME, and its coat protein was analyzed by SDS-polyacrylamide gel electrophoresis in the discontinuous buffer system of Laemmli⁶⁾. Electrophoresis was carried out in 10% gel and the gel was stained with Coomassie Brilliant Blue R-250. For estimation of the molecular weight, the following markers were used: rabbit muscle phosphorylase b (M_r 94 K), bovine serum albumin (67 K), ovalbumin (43 K), bovine erythrocyte carbonic anhydrase (30 K), soybean trypsin inhibitor (20.1 K), bovine alpha-lactalbumin (14.4 K), all from Pharmacia P-L Biochemical.

RESULTS

Isolation of ALMV

ALMV was detected together with HiMV, NeLV and CMV from a *E. grandiflora* plant showing mosaic symptoms. Since no proper differential plants for ALMV were found in preliminary inoculation tests, ALMV was isolated by serial transfer of single local lesion produced on *C. quinoa* leaves. The ALMV culture was shown to be free from HiMV, NeLV and CMV by serological tests.

Symptomatology and host range

Three to four weeks after inoculation of ALMV to virus-free plants of *E. grandiflora*, distinct mosaic symptoms appeared on the newly developed leaves (Fig. 2b), while no visible symptoms were observed on the inoculated leaves. Flower stalks and bracts also showed mosaic symptoms. Flower petals of the inoculated plants exhibited several tiny etched flecks along veins, and were slightly distorted (Fig. 2a). These symptoms, especially on flowers, were much less severe than those of a plant from which ALMV was originally isolated. Of 42 species inoculated, in addition to *E. grandiflora*, *Nicotiana benthamiana* was infected systemically and showed mosaic symptoms. *C. quinoa* and *C. amaranticolor* developed necrotic local lesions about 7 days after inoculation. The following plant species and cultivars were not infected: *Abelmoschus esculentus* 'Better five', *Arachis hypogaea*, *Beta vulgaris* var. *Cicla*, *Brassica rapa* 'Kanamachikokabu', *Capsicum annuum* 'Ace', *Chrysanthemum coronarium*, *Cucumis melo* var. *conomon* 'Daitokyo-sirouri', *C. melo* var. *reticulatus* 'New melon', *C. sativus* 'Sagamihanjiro', *Cucurbita maxima* 'Tokyo', *C. moschata* 'Kinsi', *Datura stramonium*, *Glycine max* 'Tsurunoko', *Gomphrena globosa*, *Hippeastrum* $\times$ *hybridum*, *Lagenaria siceraria*, *Lilium* $\times$ *formolongi* 'Ginga', *Lycopersicon esculentum* 'Fukuju No. 2', *Nerine sarniensis*, *Nicotiana clevelandii*, *N. debneyi*, *N. glauca*, *N. glutinosa*, *N. rustica*, *N. tabacum* 'Bright Yellow', *Petunia* $\times$ *hybrida*, *Phaseolus vulgaris* 'Yamasirokurosando', *Pisum sativum* 'Fukkoku', *Raphanus sativus* 'Kameido', *Sesamum indicum*, *Solanum melongena* 'Senryo', *Spinacia oleracea* 'Try', *Tetragonia expansa*, *Trifolium repens*, *Vicia faba* 'Wase', *Vigna angularis* 'Kyotodainagon', *Vigna sinensis* var. *sesquipedalis* 'Kurodanesanjaku', and *Zinnia elegans*.

Aphid transmission

M. persicae transmitted ALMV from a *E. grandiflora* plant with mosaic symptoms to four out of five virus-free *E. grandiflora* plants.

Purification

ALMV was effectively concentrated from clarified sap by PEG 6000 without major loss. Upon isopycnic centrifugation of the concentrated preparation in Cs_2SO_4 , the virus formed a single band between two bands which were presumably composed of host materials. Purified preparation, resuspended in 10 mM PB

Fig. 2. Experimental infection of virus-free *E. grandiflora* plant with ALMV. Flower petals with several tiny etched flecks and slight distortion (a). Leaves with clear mosaic symptoms (b).

Table 1. Serological reaction^{a)} of Amazon lily mosaic virus (ALMV) to 14 potyvirus antisera

Antisera	Dilution end point to ALMV (A)	Homologous titers (B)	SDI value ^{b)}
<i>Alstroemeria</i> mosaic virus	8	1024 ^{c)}	7
<i>Freesia</i> mosaic virus	— ^{d)}	1024 ^{c)}	>10
<i>Hippeastrum</i> mosaic virus (Eucharis isolate)	4	1024 ^{c)}	8
<i>Hippeastrum</i> mosaic virus	4	4096 ^{c)}	10
<i>Hyacinth</i> mosaic virus	16	1280 ^{c)}	6.3
Leek yellow stripe virus	—	1024 ^{c)}	>10
<i>Narcissus</i> yellow stripe virus	<2 ^{c)}	1024 ^{c)}	>9
Onion yellow dwarf virus	8	512 ^{c)}	6
<i>Ornithogalum</i> mosaic virus	2	320 ^{c)}	7.3
Potato virus Y	8	2048	8
<i>Scilla</i> mosaic virus	—	320 ^{c)}	>8.3
Tulip breaking virus	1	128 ^{c)}	>10.3
Turnip mosaic virus	<2	2048	>10
Watermelon mosaic virus 2	4	4096	10
Zucchini yellow mosaic virus	16	4096	8
Homologous antiserum	2048		

a) Microprecipitin test was carried out using 200 µg/ml of purified virus as antigen.

b) Serological differentiation index: $SDI = \log_2(B/A)$

c) Based on the information from the donors.

d) No reaction.

e) No reaction with diluted antiserum.

Fig. 3. Purified particles of ALMV negatively stained with 2% PTA.

(pH 7.0) showed an ultraviolet absorption profile typical of a nucleoprotein, with maximum absorption at 260 nm and minimum at 246 nm. The $A_{\max}/A_{\min}$ and A_{260}/A_{280} ratios (not corrected for light scattering) were 1.21 and 1.32, respectively. The estimated yield of virus was about 1 mg per 100 g of infected leaves of *C. quinoa* on the basis of an extinction coefficient of 2.7²⁾.

Electron microscopy

Elongated flexuous particles were easily detected in crude sap of infected leaves of *C. quinoa* and *E. grandiflora* (Fig. 3). The size of the particles was about 760 nm in length and 13 nm in width. In ultrathin sections of mesophyll cells of *E. grandiflora* infected with ALMV alone, pinwheel inclusions were observed in the cytoplasm (Fig. 4).

Fig. 4. Ultrathin section of a mesophyll cell of *E. grandiflora* plant infected with ALMV showing pinwheels.

Serology

The antiserum to ALMV prepared in this study had a homologous titer of 1:2048. Serological relationships of ALMV to other potyviruses are summarized in Table 1. ALMV did not react strongly with any of the antisera examined, but was shown to be distantly related to AIMV, HiMV, HyMV, OYDV, OMV, PVY, TBV, watermelon mosaic virus 2 (WMV-2) and zucchini yellow mosaic virus (ZYMV). Among these viruses, AIMV, HyMV and OYDV were slightly closer to ALMV than others. ALMV did not show positive reactions with antisera to BYMV, FMV, LYSV, ScMV and TuMV, though undiluted antisera were not used for BYMV and TuMV.

Fig. 5. Electrophoresis of ALMV RNA denatured with glyoxal in 1% agarose gel. Tobacco ringspot virus (TRSV) RNA and turnip mosaic virus (TuMV) RNA were used as molecular weight markers.

Nucleic acid

Nucleic acid extracted from purified ALMV migrated as a single band in 1% agarose gel electrophoresis under non-denaturing conditions. Although nucleic acid digested with DNase produced a clear band, no bands were produced after incubation with RNase. The UV-absorption profile of ALMV RNA changed by incubation with formaldehyde. There was a shift of wave length at which maximum absorption was recorded from 259 nm to 263 nm, and a hyperchromicity of 22%. These results indicated that ALMV contained a single stranded RNA genome. Molecular weight of ALMV RNA was estimated to be 3.32×10^6 under denaturing conditions with 1 M glyoxal (Fig. 5).

Coat protein

Coat protein migrated as one major band with an estimated molecular weight of 35 K. Two minor bands migrating faster than the 35 K band were also observed (Fig. 6). The minor bands were considered to correspond to breakdown products of the major band⁴.

DISCUSSION

A filamentous virus, ALMV, isolated from *E. grandiflora* showing mosaic symptoms could clearly be assigned to the potyvirus group. The value of molecular weight both for RNA (3.32×10^6) and the coat protein (35 K) of ALMV are similar to those reported for other potyviruses⁷. Particle length (about 760 nm) was typical of the potyvirus group. Inclusion bodies induced by ALMV were also characteristic to potyviruses.

Serological test indicated that ALMV was distantly

Fig. 6. Electrophoresis of ALMV coat protein in 10% polyacrylamide gel. Molecular weights of marker proteins (lane 1) were denoted on the left side. ALMV coat protein was electrophoresed in lane 2.

related to HyMV, OYDV and AIMV. More distant relationships of ALMV with HiMV, PVY, TBV, WMV-2 and ZYMV were also found. On the basis of the host range and serological data, we conclude that ALMV is a new member of the potyvirus group.

The presence of a virus with filamentous particles about 740 nm in length in *E. grandiflora* was first reported in 1964, and the virus was designated as *Eucharis* mosaic virus (EMV)¹¹. It was also described in the report that antisera to PVY and bean yellow mosaic virus reacted weakly with the crude sap of the *Eucharis* plants with mosaic symptoms. Isolation and further characterization of EMV have not been carried out. Although it was assumed that EMV was a potyvirus based on the particle length and the positive reactions with antisera to some potyviruses, inadequate data for characterization of EMV made it difficult to compare ALMV with EMV.

Jayasinghe and Dijkstra⁵ confirmed HiMV as the causal virus of mosaic disease of *E. grandiflora*. As we also detected HiMV from *E. grandiflora* plants showing mosaic symptoms simultaneously infected with ALMV (data not shown), it is suggested that cross-protection between these viruses does not occur. The identification of ALMV in this study indicated that the two different potyviruses caused mosaic disease of *E. grandiflora* by the single or the mixed infection. It remained to be determined which potyvirus is prevalent in the field.

Symptoms of *E. grandiflora* caused by ALMV alone were less severe than those of the plant from which ALMV was originally isolated. As the original diseased plant was also infected with three other viruses (HiMV, NeLV and CMV, unpublished data), additional infection of these viruses will make symptoms severer.

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和 文 摘 要

寺見文宏・本田要八郎・福本文良：アマゾンユリ *Eucharis grandiflora* から分離された新種の potyvirus, アマゾンユリモザイクウイルス

アマゾンユリ (*Eucharis grandiflora*, ヒガンバナ科) のモザイク病株から検出された長さ約 760 nm のひも状ウイルスの分離・同定を行った。病株から *Chenopodium quinoa* での単病斑分離によって得られたウイルス株は、*C. amaranticolor* に局部病斑を生じ、*Nicotiana benthamiana* に全身感染してモザイク症状を起こした。同じヒガンバナ科のアマリリスおよび *Nerine sariniensis* を含む 12 科 38 種の植物には感染が認められなかった。アマゾンユリの無毒株に本ウイルスを接種したところ、数種ウイルスが重複感染している原株よりも軽いモザイク症状が現れた。本ウイルスはモモアカアブラムシによって容易に伝搬された。アマゾンユリの感染葉の細胞質には potyvirus 特有の封入体が観察された。*C. quinoa* の感染葉から得られた純化ウイルスを用いて RNA および外被タンパクの分子量を推定した結果、それぞれ約 3.32×10^6 および約 35,000 であった。アマゾンユリで報告のあるアマリリスモザイクウイルスを含む他の 14 種の potyvirus との血清学的類縁関係を微量法により調べた結果、いずれのウイルスとも近縁ではなかった。以上の結果から、本ウイルスは未記載の potyvirus であると考えられたので、アマゾンユリモザイクウイルス Amazon lily mosaic virus と命名した。