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Characteristics of *Cucumber mosaic virus* isolated from *Zea mays* in Korea

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A virus causing mottle and stunt symptom on *Zea mays* was observed around Ulleng-do, Korea and identified as *Cucumber mosaic virus* (CMV-ZM) based upon biological, serological, and molecular characteristics. In host range studies, the CMV-ZM isolate produced local lesions on *Datura stramonium*, *Vigna unguiculata*, *Cucurbita moschata*, *Chenopodium amaranticolor*, *Ch. quinoa*, whereas this isolate produced systemic mosaic on *Nicotiana tabacum* cv. 'Xanthi-nc', *Capsicum annuum*, *Solanum lycopersicum*, *Solanum melongena*, *Cucurbita pepo*, and *Z. mays*. In addition, chlorotic local rings on inoculated leaves along with severe mosaic, malformation, and fern leaf symptoms on upper systemic leaves were shown in *N. glutinosa* plants. Complete nucleotide sequences of each genomic RNA segment was determined and compared to those of the other CMV strains. Comparison of the nucleotide sequence of 1a open reading frame (ORF) revealed approximately 89.2–92.4% sequence identity with each CMV subgroup IA and IB strain, while showing only 78% sequence identity with CMV subgroup II. Nucleotide sequence analysis of RNA2 ORFs revealed 85.3–97.6% sequence identity with subgroup I. In ORFs of RNA3, levels of nucleotide sequence identities were higher than 92–99.2% with CMV subgroup I and lower than 82% with CMV isolates of subgroup II. These results suggest that CMV-ZM isolate is more closely related to subgroup I than subgroup II and therefore, CMV-ZM isolate might be classified into as CMV subgroup I based on biological and molecular analysis.

Keywords **:** *Cucumber mosaic virus*, subgroup I, *Zea mays*

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Cucumber mosaic virus (CMV) is the type species of the genus *Cucumovirus* in the family *Bromoviridae* (Palukaitis and Garcia-Arenal, 2003). CMV has the broadest host range of among known plant viruses, infecting more than 1,200 species of plants from monocotyledons to dicotyledons (Douine et al., 1979; Kaper and Waterworth, 1981). Various kinds of symptoms are produced by CMV on different hosts (Choi et al., 2004; Jeon et al., 2006; Kaper and Waterworth, 1981; Lee et al., 2007; Lee et al., 2008; Martelli and Russo, 1985; Oh et al., 2008). CMV is efficiently transmitted by more than 75 species of aphids including *Myzus persicae* and *Aphis gossypii* in a stylet-borne, nonpersistent manner (Palukaitis et al., 1992). The genome of CMV is a single-stranded, positive-sense RNA having three RNA segments, which contain five genes encoding proteins designated 1a, 2a, 2b, 3a, and capsid protein (CP) (Ding et al., 1994; Palukaitis and Garcia-Arenal, 2003; Palukaitis et al., 1992). The numerous strains of CMV have been classified into two major groups by nucleotide sequence similarity, and subgroup I has been further divided into two subgroups by phylogenetic analyses (Aramburu et al., 2007; Chaumpluk et al., 1996; Roossinck et al., 2003).

Maize (*Zea mays*), family *Gramineae*, is widely cultivated throughout the world producing 817 million tonnes worldwide in 2009 which was more than rice or wheat (FAO, 2009). Virus disease incidences on maize were reported in all countries where maize crops were grown and the natural occurrences of more than 40 distinct viruses in maize crops including *Barley stripe mosaic virus* (BSMV), *Barley yellow dwarf virus* (BYDV), *Cucumber mosaic virus* (CMV), *Maize chlorotic dwarf virus* (MCDV), *Maize dwarf mosaic* virus (MDMV), *Maize leaf fleck virus* (MLFV), *Rice black-streaked dwarf* virus (RBSDV), and *Rice stripe virus* (RSV) were reported in the world (Damsteegt et al., 1981; Shurtleff et al., 1986; White, 1999). Some of these viruses cause occasionally serious economic damage in maize production. CMV infection on maize was first identified in 1934 in Florida and thus maize was

reported as its natural host (Wellman, 1934). In addition, natural occurrence of maize infection with CMV in Europe has been reported only in former Yugoslavia (Panjan, 1966).

In Korea, three viruses including C*ucumber mosaic virus* (Lee et al., 1982), *Maize dwarf mosaic virus* (Lee et al., 1981), and *Rice black streaked dwarf virus* (Jeong et al., 1987; Lee et al., 1978; Lee et al., 2005) have been reported on maize plants. Although CMV infection does not cause significant damage in maize production, it should not be overlooked since this virus has wide host range. In this paper, we analyzed the biological characteristics, obtained complete genome sequence, and conducted phylogenetic relationship of CMV-ZM isolate with the other CMV strains and/or isolates.

Maize plants showing irregular mosaic stripe, mottle on the leaves and stunt on the stem (Fig. 1) were collected from Uleng-island in 2006. The collected isolates identified by electron microscopy and RT-PCR using CMV specific primers (Forward; 5'-TGGTCGTCCAACTATTAACCAC-3', Reverse; 5'-TACTGATAAACCAGTACCGGTGA-3'). Quick dip preparation was used for the observation of virus particle from field collected samples. Virus particles were not observed under electron microscope (EM, LEO 912AB; Carl Zeiss, Germany) at 100 kV. General spherical viruses including CMV are difficult to observe under EM because of low concentration and similarity to the other organelles in plant cell. Virus isolate was inoculated onto *Chenopodium quinoa* and representative single lesion on inoculated plant was used as inoculum for three consecutive transfers. The single lesion from the third inoculation was then inoculated onto *Nicotiana tabacum* cv. 'Xanthi-nc' for virus propagation. Purified virus preparations stained with 0.5% uranyl acetate revealed the presence of typical isometric particles of 28–30 nm diameter (data not shown).

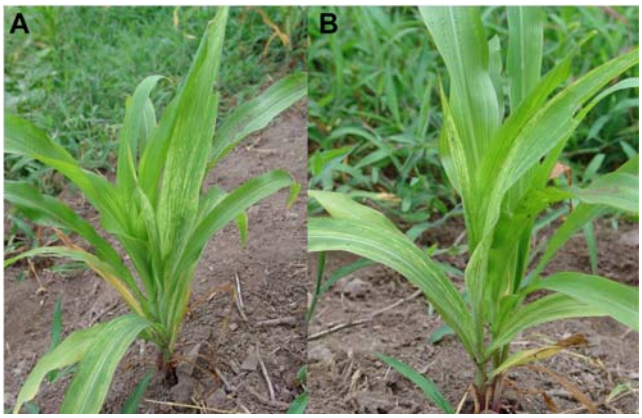

Fig. 1. Viral disease symptoms on maize plants in the field (A), and CMV-infected maize plants showing mottle and stunt (B) on leaves.

Virus was purified from the inoculated *Nicotiana tabacum* cv. 'Xanthi-nc' as described previously (Palukaitis et al., 1992) and the purified CMV isolate, named as CMV-ZM isolate, was subjected to biological and molecular analyses. For symptom evaluation, the CMV-ZM was mechanically inoculated onto 14 different plant species belonging to *Solanaceae*, *Leguminosae*, *Chenopodiaceae*, *Brassicaceae, Cucurbitaceae*, and *Gramineae*. Symptoms caused by CMV-ZM on tested plants were compared with those caused by CMV-Z and -RB (Kim et al., 2010a, 2010b). Symptom appearance induced by the CMV-ZM along with CMV-Z and CMV-RB were observed from at least 10 plants per tested species collected from three independent experiments. Inoculated plants were maintained in an insect-free greenhouse at 20–25 °C. Symptoms were observed for 3–4

Table 1. Symptoms developed on indicator plants that were mechanically inoculated with *Cucumber mosaic virus* isolate ZM (CMV-ZM)

Indicator plants	Symptoms[a] on the leaves (inoculated/upper)		
	CMV-ZM	CMV-Z[b]	CMV-RB[c]
Solanaceae			
Nicotiana tabacum cv. 'Xanthi-nc'	cl/vc,m	cl/m	cl/m
N. glutinosa	crl/sm,f	cl/m	–/m
Capsicum annuum	cl/cl,m	–/m	–/vc
Solanum lycopersicum	–/ m	–/m,mal	–/m
Datura stramonium	cl/–	crl/–	cl/–
Solanum melongena	–/m	cl/m	cl/vc,m
Leguminosae			
Vigna unguiculata	pp/–	nl/–	pp/–
Phaseolus angularis	–/–	–/m	–/m
Cucurbitaceae			
Cucurbita pepo 'Taeyang'	cl/cl,st	cl/sm, st	cl/sm,mal
Cu. moschata 'Jinhan Aihobag'	cl/–	cl/vc	–/–
Brassicaceae			
Brassica pekinensis L.	–/–	–/–	–/–
Raphanus sativus L.	–/–	–/–	–/–
Chenopodiaceae			
Chenopodium. amaranticolor	nl/–	nl/–	nl/–
Ch. quinoa	nl/–	nl/–	pp/–

[a] cl, chlorotic local; nl, necrotic local; crl, chlorotic ring local; pp, pin point; vc, vein clearing; m, mosaic; sm, severe mosaic; f, fern leaves; st, stunt; mal, malformation; –, no symptom.
[b] CMV-Z, *Cucumber mosaic virus* - Zucchini (Kim et al., 2010b)
[c] CMV-RB, *Cucumber mosaic virus* - *Rudbeckia bicolor* (Kim et al., 2010a)

weeks post inoculation. CMV infection was confirmed by symptom appearance and by enzyme linked immunosorbent assay (ELISA) using ELISA test kits purchased from Agdia (USA; Hsu et al., 2000). Absorbance at 405nm was measured with a model microplate Reader (EL312e EIA; Bio-Tek, USA).

CMV induces a variety of symptoms depending on the host plant species and on the virus strain. Host range and symptoms on tested plants by CMV-ZM were summarized in Table 1. CMV-ZM caused systemic infection in *N. tabacum* cv. 'Xanthi-nc', *N. glutinosa*, *Capsicum annuum*, *Solanum esculentum*, *Solanum melongena*, *Cucurbita pepo* and local infection in *Datura stramonium*, *Vigna unguiculata*, *Cu. moschata*, *Chenopodium amaranticolor*, and *Ch. quinoa* (Fig. 2). However, CMV-ZM isolate failed to infect and induce symptoms in *Brassica campestris*, *Raphanus sativus*, and *Phaseolus angularis*. The experimental host range of CMV-ZM was similar to that reported for CMV-Fny isolate (Palukaitis et al., 1992). The host range and symptoms of CMV-ZM differ in some respect from previous reported CMV-Z and -RB isolates (Kim et al., 2010a, 2010b). Comparing symptoms of those CMV isolates, CMV-ZM induced chlorotic local ring on inoculated leaves of *N. glutinosa*. However, systemic symptoms were similar to those caused by the other two isolates. The necrotic ringspot symptom on inoculated leaves has been reported in CMV lily isolates (CMV-Ly2 and-Ly8) on *N. tabacum* cv. 'Xanthi-nc', but necrotic ringspot symptom on upper non-inoculated leaves was only observed from CMV-Ly8 (Lee et al., 2007). CMV-Z, -RB, and CMV-ZM also differed significantly in their pathogenicity on *P. angularis*, *Cu. moschata* (Green pumpkin), and *Z. mays*. CMV-ZM did not induce systemic symptoms on *Phaseolus angularis* whereas systemically symptoms were observed from CMV-Z and -RB infected leaves. CMV-ZM and -RB do not cause a systemic infection in *Cu. moschata.* On the other hand, CMV-Z isolate was obtained from *Cu. pepo*, which showed vein clearing symptom on upper non-inoculated leaves. Interestingly, only CMV-ZM isolate caused systemic infection causing mottle, yellowing stripe, stunt on *Z. mays* leaves (Table 2; Fig. 2). However, CMV-Z and -RB isolates did not induce a systemic infection on upper leaves in *Z. mays*. Although some CMV isolates can infect *Z. mays* plant (Douine et al., 1979; Wahyuni et al., 1992; Ryu et al., 1998), natural CMV infection on *Z. mays* was rarely observed. Altogether, these three tested CMV isolates showed clear differences in host reaction of specific plant species. CMV-ZM isolate induce systemic symptoms in *Z. mays* but did not cause systemic symptoms in *P. angularis*. Thus, these differences are considered as unique characteristics of CMV-ZM.

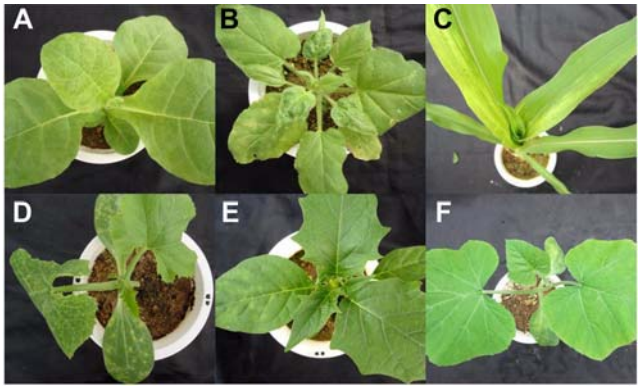

Fig. 2. CMV-ZM induced chlorotic local lesions in inoculated leaves and systemic spotting or mosaic in *Nicotiana tabacum* cv. Xanthi-nc (A), *N. glutinosa* (B), *Zea mays* (C), and *Cucurbita pepo* (D) whereas only chlorotic local lesions were formed *Datura stramonium* (E) and *Cucurbita moschata* (F).

The total RNAs were extracted using the total RNA kit (iNtRON, Korea) from leaves of purified virus preparation. To amplify complete genomic regions, a two-step Reverse Transcription-Polymerase Chain Reaction (RT-PCR) protocol was used. The first strand cDNA was synthesized with AMV reverse transcriptase (Promega, USA) and subjected to thermocycling amplification using LA *Taq* DNA polymerase (TaKaRa, Japan). The primers were designed to sequence full length genome of each segments based on the previously reported CMV sequences available in GenBank of NCBI (Kim et al., 2010a, 2010b). The PCR products were purified using PCR gel/direct extraction kit (iNtRON, Korea) and cloned into pGEM-T easy vector (Promega, USA) according to the manufacturer's instructions followed by transformation into *Escherichia coli* JM109. Complete nucleotide sequences of each genomic RNA segment were determined and submitted to GenBank (accession no. JN180309, JN180310, JN180311). The sequences were then compared to equivalent sequences from a range of other CMV isolates gene present in GenBank. Multiple nucleotide sequence alignments were performed by using Clustal W (Geneious pro 5.13). Assembled nucleotide sequences and the deduced amino acid sequences were

Table 2. Comparative analysis of infectivity of CMV isolates in maize

CMV isolates	Symptoms[a] on the leaves	
	Inoculated	Upper
CMV-Z	cl (7/12)	– (0/12)
CMV-RB	cl (9/12)	– (0/12)
CMV-ZM	cl (12/12)	mo,yst, st (12/12)

[a] cl, chlorotic local; mo, mottle; yst, yellowing stripe; st, stunt; –, no symptom.

Table 3. Nucleotide/amino acid sequence identities (%) between CMV-ZM and the previously reported strains of CMV

Isolate	Strains[a]	Nucleotide and amino acid identity (%)				
		RNA1	RNA2		RNA3	
		1a	2a	2b	3a	Cp
CMV-ZM	CMV-Fny	91.7/97.8	96.8/97.5	97.3/97.3	97.6/99.3	99.2/100
	CMV-Mf	92.4/97.1	96.6/97.2	96.1/97.3	97.5/99.3	98.0/99.5
	CMV-Leg	91.8/97.0	96.2/96.8	93.1/85.5	98.0/99.6	97.7/98.2
	CMV-Tfn	91.3/97.4	92.1/93.6	87.9/81.7	93.9/96.8	95.4/99.1
	CMV-Y	91.2/96.1	97.0/97.9	97.6/96.4	97.9/99.6	97.6/97.2
	CMV-Z	92.3/98.0	96.3/96.8	96.4/95.5	96.2/99.3	97.0/98.6
	CMV-RB	92.5/96.0	96.3/96.8	97.3/98.2	97.0/99.3	98.6/99.5
	CMV-NT9	91.5/97.5	92.1/93.8	87.9/81.7	93.7/96.8	95.1/98.6
	CMV-Ix	90.8/96.5	90.7/92.6	86.7/80.0	92.0/94.3	92.7/95.9
	CMV-IA	89.2/94.4	90.6/91.8	85.3/74.5	92.5/96.1	92.5/97.7
	CMV-CTL	90.8/95.8	91.5/94.4	88.0/82.7	94.1/96.0	93.0/97.7
	CMV-Ls	78.2/85.5	73.1/76.6	64.7/53.5	78.9/83.2	76.9/82.0
	CMV-Ly	78.1/85.0	73.2/76.0	64.4/52.5	78.7/83.5	76.6/82.5
	CMV-Trk7	78.2/85.3	73.1/76.3	65.3/53.5	78.6/83.9	76.1/80.6
	CMV-Q	78.2/84.9	73.1/75.1	64.0/53.5	79.1/83.2	77.2/82.9

[a] The Genbank accession number of the reference CMV isolates: ZM(JN180309, JN180310, JN180311); Fny (D00356, D00355, D10538); Mf (AJ276479, AJ276480, AJ276481); Leg(D16403, D16406, D16405); Tfn (Y16924, Y16925, Y19626); Y (D12537, D12538, D12499); Z (GU327366, GU327367, GU327368); RB (GU327363, GU327364, GU327365); NT9 (D28778, D28779, D28780); Ix (Y20220, U20218, U20219); IA (AB042292, AB042293, AB042294); CTL (EF213023, EF213024, EF213025); Ls (F416899, AF416900, AF127976); Ly (AF198101, AF198102, AF198103); Trk7 (AJ007933, AJ007934, L15336); Q (X02733, X00985, M21464). Standard subgroup I isolates are Fny, Mf, Leg, Tfn, Y, NT9, Ix, IA and CTL. Standard subgroup II CMV isolates are Ls, Ly, Trk7 and Q.

analyzed using the software package Mega 5.0, DNAMan 4.02, and Geneious pro 5.13. Phylogenetic analyses were performed employing Maximum likehood method that is packaged in the MEGA 5.0 software (Nei et al., 2000).

Comparative sequence analysis disclosed that the 1a, 2a, 2b, 3a, and CP ORFs of CMV-ZM had 89.2–92.5%, 90.6–97%, 85.3–97.6%, 92–98%, and 92.5–99.2% sequence identity, respectively, with CMV subgroup I isolates at the nucleotide level (Table 3). In contrast, identities of 64 to 79.1% were observed with subgroup II isolates at the nucleotide level. Amino acid sequences analysis of five ORFs of CMV-ZM and subgroup I isolates showed about 74.5-100% sequence identity. In CMV-ZM, 1a ORF showed highest sequence identity at nucleotide level with the CMV-Mf isolate (92.4%) and two ORFs of RNA2 showed 97 and 97.6% sequence identity with the CMV-Y isolate. The 3a and CP ORFs showed sequences identity of 98 and 99.2%, with the CMV-Leg and -Fny isolates, respectively. Nucleotide and amino acid sequences of five ORF genes of CMV infecting *Zea mays* showed greatest identity with CMV subgroup I isolates.

The phylogenetic tree was divided into two large groups (subgroup I and II) based on nucleotide sequences of RNAs 1, 2 and 3 (Fig. 3). In addition, the RNA2 and 3 was clearly subdivided into two subgroups IA and IB, however, these further divergences were not obvious in phylogenetic analysis of RNA1. CMV-ZM isolate was more closely clustered with CMV-RB isolate of subgroup I in the RNA1. Analysis of RNA2 and 3 revealed mono-phyletic clustering with subgroup IA. The homology of the ORF was over 95% in subgroup IA isolates except 1a gene. CMV subgroup I is subdivided further into IA and IB on the basis of gene sequences and phylogenetic relationships (Palukaitis and Zaitlin 1997; Roossinck 2002). CMV-ZM showed more than 90% sequences identity at the nucleotide level with subgroup IB.

Relationship of three CMV isolates was compared using pathogenicity to host plants and multiple alignment analyses of the five ORFs (1a, 2a, 2b, 3a, and CP; data not shown). The amino acid sequence analysis of CMV-Z and -RB with CMV-ZM showed higher than 95.5% sequence identity. Several amino acid variations were found in 1a gene. Amino acids sequence alignment of 1a gene between CMV-ZM, CMV-Z, and -RB showed 2 differences from position 468 (Ala to Val) and 900 (Ser to Ala). For 2a protein sequences, these three isolates had two unique variations, the 3th Phe to Ser and the 804th Ala to Thr. In this regard, it is worth mentioning that the amino acid variations on 2a of RNA2 were reported to be responsible for causing systemic symptoms on maize (Rao et al., 1982). The

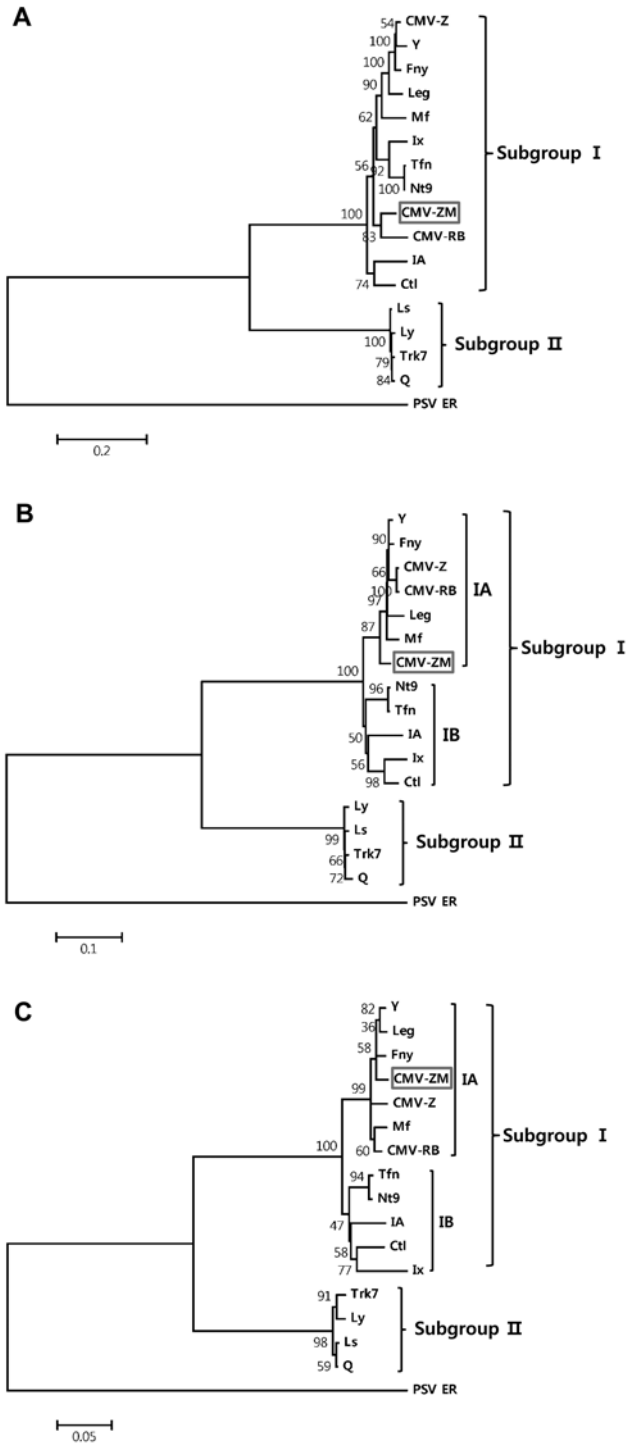

Fig. 3. Maximum likehood method phylogenetic trees base on MEGA 5.0 software derived from nucleotide sequences of the RNA segments 1, 2 and 3 of CMV-ZM with previously reported CMV isolates (panels A, B, and C, respectively). *Peanut stunt virus* (PSV) was used as an outgroup.

variations of amino acids were not observed in 2b, 3a, and CP genes (data not shown). The sequence(s) and/or genes in RNA3 have been reported to be related in resistance breaking in maize (Marchoux et al. 1975; Ryu et al., 1998). However, we could not find corresponding amino acid sequence variations in RNA3. These results suggest that the other region and/or genes of CMV are also involved in pathgenicity and thus indicating that complex variations are involved in the pathogenicity of CMV.

Although CMV has one of the widest host ranges among all plant viruses, including a great number of dicotyledonous plants, only a few monocotyledonous plants are reported as hosts. The sudden occurrence of CMV in monocotyledonous may be associated with the widespread occurrence of aphids since the abundance of the birdcherry oat aphid (*Rhopalosiphum padi*) increased in maize in Korea (Lee et al., 1992; Yoon et al., 1974). Results of this study indicated that the virus isolate causing stripe, mottle and stunt symptoms on maize was identified as CMV-ZM belonging to subgroup I based upon biological and molecular analyses. This is the first reported sequence of an isolate of CMV naturally occurring in maize. Further molecular characterization by constructing and analyzing infectious clones will be required for identification of sequences and/or genes involved in pathogeniciy.

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