Complete Genome Sequence of the First Chrysovirus From the Phytopathogenic Fungus *Alternaria Solani* on Potato in China

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Abstract

The full genome of a double-stranded RNA (dsRNA) mycovirus, which was isolated from *Alternaria solani* strain DT-10 causing potato foliar disease and designated as *Alternaria solani* chrysovirus 1 (AsCV1), consisted of four dsRNA segments (dsRNA 1–4) with the length of 3600 bp, 3128 bp, 2996 bp, and 2714 bp, respectively. RNA-dependent RNA polymerase (RdRp, 1084 amino acids (aa)), putative capsid protein (905 aa), Alphachryso-P3 (835 aa), and Alphachryso-P4 (729 aa) were encoded by dsRNA1, dsRNA2, dsRNA3, and dsRNA4, respectively, which had the highest identities of 41.77%-72.38% to the counterparts of *Helminthosporium victoriae virus 145S* (HvV145S) in the genus *Alphachrysovirus* of the family *Chrysoviridae*. Moreover, the 5'-untranslated regions (UTRs) with several unique inserts (3–37 bp) and deletions (5–64 bp) of AsCV1 dsRNA 1–4 shared 51.65%-68.01% identities to those of HvV145S. Phylogenetic analysis of RdRp suggested that AsCV1 clustered the most closely with HvV145S. Based on the characteristics of distinct host, low identities of encoded proteins, special traits in 5'-UTRs of dsRNA 1–4, and phylogenetic analysis of RdRp, AsCV1 was confirmed to be a new species in the genus *Alphachrysovirus*. To our best knowledge, this is the first alphachrysovirus identified from phytopathogenic *A. solani*.

Introduction

Mycoviruses identified in fungi and oomycetes, have genomic types of double-stranded RNA (dsRNA), single-stranded RNA (ssRNA), and DNA [1]. DsRNA mycoviruses belong to seven families including *Birnaviridae*, *Chrysoviridae*, *Cystoviridae*, *Megabirnaviridae*, *Partitiviridae*, *Picobirnaviridae*, and *Quadriviridae*, and a new established genus *Botybirnavirus* [2, 3]. The family *Chrysoviridae* contains two genera, namely *Alphachrysovirus* (17 species) and *Betachrysovirus* (8 species). Members of *Chrysoviridae* possess 3–7 dsRNA segments with each segment being separately encapsulated. Among these dsRNA segments, the dsRNA1 and dsRNA2 encodes RNA-dependent RNA polymerase (RdRp) and capsid protein (CP), respectively. Virions of chrysoviruses, whose hosts include fungi, plants, and insects, are isometric and non-enveloped, with the size of about 40 nm in diameter [4, 5].

In 1988, viral dsRNAs were detected in *Alternaria alternata* isolated from Japanese pear trees, which is the first reported mycovirus in *Alternaria* [6]. Later, many mycoviruses had been identified in *A. alternata*, such as *Alternaria alternata virus-1* (AAV-1) [7], *Alternaria alternata chrysovirus 1* (AaCV1) [8], *Alternaria alternata partitivirus 1* (AtPV1) [9], *Alternaria alternata botybirnavirus 1* (AaBRV1) [3], and *Alternaria alternata hypovirus 1* (AaHV1) [10]. In addition, several mycoviruses including *Alternaria tenuissima partitivirus 1* (AttPV1) [11], *Alternaria brassicicola endornavirus 1* (AbEV1) [12], *Alternaria longipes dsRNA virus 1* (AlRV1) [13], *Alternaria arborescens victorivirus 1* (AaVV1) [14], and *Alternaria dianthicola dsRNA virus 1* (AdRV1) [15] had been reported in five other species (*A. tenuissima*, *A. brassicicola*, *A. longipes*, *A. arborescens*, and *A. dianthicola*) of *Alternaria*. Recently, an ssRNA mycovirus named *Alternaria solani fusarivirus 1* (AsFV1) had been isolated from *A. solani* [16].

In our previous study, *A. solani* had been documented to cause potato early blight in China [17, 18]. In this study, *A. solani* strain DT-10, which was recovered from diseased leaves of potato with the symptoms of early blight in Datong city, Shanxi province of China, was identified according to the methods described previously [17, 18]. A new alphachrysovirus was found to be associated with the *A. solani* strain DT-10 and designated as *Alternaria solani* chrysovirus 1 (AsCV1).

Provenance of the virus material

Alternaria solani strain DT-10 was cultured on potato dextrose agar (PDA) plates overlaid with cellophane membranes for 7 days in the dark at 25°C. Multiple dsRNAs were extracted from the mycelia by binding to the CF-11 cellulose powder in 15% ethanol as described by Morris and Dodds [19]. After treatment with S1 nuclease and DNase I (TaKaRa, Dalian, China), the dsRNAs were analyzed by 1.0% agarose gel electrophoresis (Fig. 1A) and purified with a gel extraction kit (Aidlab Biotechnologies, Beijing, China). The partial complementary DNA (cDNA) sequences of the dsRNA segments were obtained and assembled as described previously [20]. Using specific primers designed based on the obtained sequences of cDNA (Supplementary Table 1), the terminal sequences were determined by RNA-ligase-mediated rapid amplification of cDNA ends (RLM-RACE) method as described previously [21, 22]. The full genome sequences of AsCV1 were obtained through assembling all the partial cDNA and terminal sequences with DNAMAN 7.0 (Lynnon Biosoft, USA), and deposited into the GenBank database with the accession numbers of MW656210, MW656211, MW656212, and MW656213 for dsRNA1, dsRNA2, dsRNA3, and dsRNA4, respectively.

Sequence properties

The full sequence of the four dsRNA fragments are 3,600 bp, 3,128 bp, 2,996 bp, and 2,714 bp, respectively. The open reading frame (ORF) of each dsRNA sequence was analyzed using ORFfinder online tool (<https://www.ncbi.nlm.nih.gov/orffinder/>). Each dsRNA contains a single ORF, which was named ORF1, ORF2, ORF3, and ORF4 for dsRNA1, dsRNA2, dsRNA3, and dsRNA4, respectively (Fig. 1B). BLASTp search for the four ORFs resulted in the highest similarity to the counterparts of *Helminthosporium victoriae virus 145S* (HvV145S) in the genus *Alphachrysovirus* of the family *Chrysoviridae*. ORF1 encoded a protein of 1084 amino acids (aa) (124.56 kDa) with 72.38% sequence similarity to the RdRp of HvV145S-A9 (GenBank No. NC_005978). The predicted RdRp domain at 351–803 aa contained eight conserved motifs (Supplementary Fig. 1A). The protein encoded by ORF2 contained 905 aa (102.29 kDa), which showed 61.40% sequence identity to the putative CP of Bipolaris maydis chrysovirus 1 (BmCV1) (GenBank No. KY489955), an isolate of HvV145S [23]. BLASTp also presented that ORF3-encoded protein (835 aa, 92.84 kDa) and ORF4-encoded protein (729 aa, 82.31 kDa) had 69.84% identity to Alphachryso-P3 of HvV145S-A9 and 41.77% identity to Alphachryso-P4 of BmCV1, respectively.

The 5'-untranslated regions (UTRs) and 3'-UTRs of AsCV1 were 242 bp and 103 bp long in dsRNA1, 312 bp and 98 bp long in dsRNA2, 317 bp and 171 bp long in dsRNA3, and 315 bp and 209 bp long in dsRNA4, respectively (Supplementary Table 2). Multiple alignments of the 5'-UTR and 3'-UTR sequences

of the four dsRNAs were performed using DNAMAN 7.0 (Lynnon Biosoft). The 5'-UTRs presented strong sequence similarities in their internal parts, sharing strictly conserved terminal sequence of CGATAAAACAAAAA. Meanwhile, the 3'-UTRs among the four dsRNA segments shared conserved GCTTTAAGTGT termini (Supplementary Fig. 1B). The 5'-UTRs and 3'-UTRs of AsCV1 dsRNA1-4 had 51.65%-68.01% and 30.04%-70.34% identities to those of HvV145S-A9 and BmCV1. Intriguingly, several unique inserts (3–37 bp) and deletions (5–64 bp) were found in 5'-UTRs of AsCV1, which were different from those of HvV145S-A9 and BmCV1 (Fig. 2).

The RdRp sequences of AsCV1 and 24 members of the family *Chrysoviridae* were analyzed by ClustalX 2.0 and MEGA 6.0 [22]. The phylogenetic tree constructed by the neighbor-joining algorithm with 1000 replicates based on the RdRp sequences showed that AsCV1 formed a well-supported taxonomic cluster with the members of the genus *Alphachrysovirus* and was closely related to HvV145S-A9 and BmCV1 (Fig. 1C).

Virion particles were extracted from the mycelium of *A. solani* strain DT-10 and stained according to the methods previously described [24, 3]. Viewed under transmission electron microscope (TEM) (JEM-1230, JEOL, Tokyo, Japan), the particles of AsCV1 were isometric with a diameter of approximately 40 nm (Supplementary Fig. 1C).

According to ICTV, the host of isolation, nucleotide and deduced amino acid sequence data, the length of genome segments, and 5'-UTRs are useful species demarcation criteria for the genus *Alphachrysovirus* [4]. Based on host fungus *A. solani*, low sequence identities of proteins encoded, unusual characteristics of 5'-UTRs, and phylogenetic relationships to known members of *Alphachrysovirus*, AsCV1 is a novel member in the genus *Alphachrysovirus*. This is the first report of the complete genome sequence of a new chrysovirus infecting *A. solani*.

Declarations

Compliance with ethical standards

Funding: This work was financially supported by National Key Research and Development Program of China (2018YFD0200803).

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical approval: This study did not include experiments with human participants or animals performed by any of the authors.

Informed consent: Informed consent was obtained from all individual participants included in this study.

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Figures

Figure 1

Agarose gel electrophoresis, genomic organization, and phylogeny of *Alternaria solani* chrysovirus 1 (AsCV1) from phytopathogenic *Alternaria solani* strain DT-10. (A) The dsRNAs from *A. solani* strain DT-10 were resolved in 1.0% agarose gel electrophoresis. Lane M, DL 5,000 DNA Marker; Lane 1, dsRNAs extracted from *A. solani* strain DT-10 and treated with S1 nuclease and DNase I. (B) Schematic diagram of the genome organization of AsCV1. The 5'-untranslated regions (UTRs), 3'-UTRs, and open reading frames (ORFs) were noted. The yellow region represents the conserved domain of RNA-dependent RNA polymerase (RdRp). (C) A phylogenetic tree based on the RdRp sequences of AsCV1 and 24 members of the family Chrysoviridae. The tree was constructed by neighbor-joining algorithm with bootstrapping analysis of 1000 replicates in MEGA6.0, and bootstrap values higher than 50% were shown. The scale bar represents a genetic distance of 0.1, and the red star indicates AsCV1.

AsCV1	CGATAAAAAAGAAAAATTAACCAAAATCAAGTTTTATCACACAAACTGAGGCAATTATTATTAA	112
HvV145S-A9	GATAAAAAAGAAAAATTCATGAGGCAC.....AGAGGTGACAAAAGAGAACAAATTAAGTTGG...ATTTTGA	74
BmCV1	CGATAAAAAAGAAAAATTCGAATTCAG.....CGACAAAACAACTCTGATGTATTAAAGTACAATTTATTTAAATAGAATTAA	78
AsCV1	TGGCACGAGGTACTTTTCGAGCCACCTGAGGAGTAGCACTCAGGGTCACGAAACCGTGGTCGTAGTGGCGGAAAACTCATTGTAAACAC	225
HvV145S-A9	TTATTTAATTTAGTTTCGAGCTCCCTGAAGAGTAGTGCCTCAGGGCCACGAAACCGTGGTCGTAGTGGCGGAAACAACTGTGGTAAACAA	187
BmCV1	AGAAATAAATATATTTCGAGCTCCCTGAAGAGTAGTGCCTCAGGGCCACGAAACCGTGGTCGTAGTGGCGGAAACAAATTAATTGATTGAGAGAACACAAACATAACAAAGAAACA	193
AsCV1	...AAGAACAAACAAAACAAG	242
HvV145S-A9	TCTAAGAACAAATCGAACACA	207
BmCV1	AGCTAAGAACAAAC.....	205

AsCV1	CGATAAAAAACAAAAATACCTCTCTTTTGTGTTTACCAACTACAAG CTACTCAAGAGAAAAAGAGCAATTTTACTTAACTAATAATATAATATATATATATATTTAA	110
BmCV1	TGATAAAAAACAAAAATCGG TTTGGCAGGACAGACACAGTTAGGAAAACTCTGACTTGAAAAAGAGAGTTTCAAAAGTCTAATAATAAATAT	92
HvV145S-A9	GATAAAAAACAAAAATCGCT AG GCATGGAGAGAAAACTAAGAACAAATGCAGTTTGAAATAGATTAAAAACAATTAAATTTGTTAAT	86
AsCV1	TAAAT . . . CGGTCTCTCGCGTGGCGGAAAGAGTTTTCGAGCCACTGTATGATAGTACACCTCAGGGTCACGAAACCGCTGGTCGTATGTCGCGGAAAAACATTATTGTAACACAGA	222
BmCV1	TAATAATTAGACTGAATGTCTGGCAGAGTTGCATCTCGAGCCGTCTGATGATAGTACACCTCAGGGTCACGAAACCGCTGCAGCTAACGGCGGAACAGATTATTGAGGTTAGTAA	207
HvV145S-A9	TTAATTAACTATTGAATGTCTGGCAGAGTTAGACTCTCGAGCCGTCTGATGATAGTACACCTCAGGGTCACGAAACCGTGCAGCTAACGGCGGAACAGATTATTGAGGTTAGTAA	201
AsCV1	TTTGAACC . . CAGAGCTATTAAGCAAAACAACCTATACACAAAGAGAAACAACAAGAAACAAGAAACGATCAGCTCGATAGGCATCAAG	312
BmCV1	GAACACTTATCAAAACAACAACAACACACAAGG AAAACAACAACAACAACAACAACAACAAGTCGTAAC	290
HvV145S-A9	GAACACTTTCAGAACACAACAACAACAACAATAACAACAAGAAACAACAACAACAACAACAACAACAACACTGTCAACAAACAA	293

AsCV1	★	CGATAAAAAACAAAATAACCATTCCTGTTTTCATCAATAACAACACAGAGGGAATAGTITATGGAACCTCAGATTAGCTATTAAAGATCAATTTAAAACTGAATAAGTATTTAA	115
BmCV1		CGATAAAAACACAAAATCGCATAGCA CGACAACAGATAGTGGCGAATTGTITAAAAACAGATTTCAGATCACTTATATAATAAATATTITAA AT	93
HvV145S-A9		 GATAAAAAACACAAAATCGCATGGTA GACAGAGGCTGTTAAGAAACAAAACATCCAAATCAATTTAAAAACATATTTAGCTGAATAAATAAA TA	92
AsCV1	★	CAAATATTACATCATATTAAAGTGGTCTGGCCATCAAAAGTTTTCGAGCCACTGACGAGTAGAGCCTCAGGGTCACGAAACGCTGGTCTGATGTCGCGGAAACAACTTATTGTAA	230
BmCV1		CAAAATTAAGTTGGTGTCTTGGCTGGCTGGTCCAGAACAAAGTTGTCGAGCCGTCTGATGAGTAGACCACTCAGGGTCACGAAACGCTGGACGTAAACGGCGGAACAGATTATTGAGG	208
HvV145S-A9		TAATTTTAGAGAACGTTGGCTGCTGGCC AGCTTACTGTCGAGCCGTCTGATGAGTAGACCACTCAGGGTCACGAAACGCTGGACGTAAACGGCGGAACAGATTATTGAGG	201
AsCV1	★	CAC AGATTTTGAACCCACACGGAACAACGAACAACAACAACCAACAAACACAAAC AAGCAACAAGAACAACAATGCAACAAG	317
BmCV1		TTATGTAGAACAATTATACGAAACAAAAACAACAACAACAATACACAAACAACGCAACAAC AACATCCAAAGACAAGCACTAGAGGTTAGCAATGCAAC	307
HvV145S-A9		TTAGTAGAACAATTTATCAAAACACACACACACAACAACAATTAACAACAACGAACAACAACAACAACAAGAACAAGAAAGCAATAGCTTTGCAAAATACAA	302

Accession	Gene	Protein	Position	Sequence	Score
AsCV1	BmCV1 HvV145S-A9	HvV145S-A9	53	CGATAAAACAAAAATACCATTCGCTTTTATGATTAACACACAGAGGCA	53
52			TGATAAAACAGAAATTCGGAATCGACAAACATAACACGATTGAGAATATAG	52	
115			GATAAAACAGAAATCCGATAACTCGACGGCGAATTGATCAATATCACACGGATCAGTTCGAAATTCAGGATACATAAACAATTTACAGATTAAATTTCTATATAGTGAGTTG	115	
AsCV1	BmCV1 HvV145S-A9	HvV145S-A9	167	ATAAGTTT. ATGGAACACTGAGATTAGGTATTAAGATCATTTAAACGTAATAGTATTTAAACAAATATTACATCATATTAAGTGGTCTGCCACATCAAGATTTTCGAGCGCA	167
155			GTATATATT. TAAGAAATCGTGATTAACACAACCTTGTAATAATTTAATGTAATTAATTTGTTTTCAGAGT. TAAGTACCTGCTCTGGTGCAGTGATTTTCGAGCGCG	155	
218			GTTTGAGTACTGAACATACACAATTGACAGGTGGTGGAAACACACAGATAAGTCAATGGGTAAATATCC. TAACCTTCTCTGCTGTGACAGCAAGTTCGTCGAGCGCG	218	
AsCV1	BmCV1 HvV145S-A9	HvV145S-A9	281	CCTGACGAGTACAGCCTCAGGGTACGAAACGCTGGTCGTAGTGGCGGAACAACTTATTTGTAACACAGACTTATATCAACAACACAAAGCAAGCAAGATAGCAAAATCAACA	281
269			TCTGATGAGTAGCACTCTCAGGGTACGAAACGCTGGACGTAAAGGGCGGAACAGATTAATTCAGGTTAGTAACTATTCGAACAACACAAACAAACAACATTGACAACA	269	
333			TCTGATGAGTAGCACTCTCAGGGTACGAAACGCTGGTCGTAAAGGGCGGAACAGATTAATTCAGGTTAGTAACTATTCGAACAACACAAACAAACAACAAACAACAAACATCAACA	333	
AsCV1	BmCV1 HvV145S-A9	HvV145S-A9	315	CAGAACAAACAACAGGAACAAACAATACAACAG	315
368			ACAACACATACAACACAAGCAGAACACACTCAAGTCAAAAGGACTTACAAAACACACATCAACTTGAACCCCAATCAAAGTTAAATCAAC	368	
412			CAACAACAACAACAACAGCAGACAACAACATTTGCTAGTTTGTCAAGTTCTAAATAGGATCAACAACAACTACAAGCAAAA	412	

Supplementary Files

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- [SupplementaryFig.1.tif](#)
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