ANNOTATED SEQUENCE RECORD



Complete genome sequence of a novel secovirid infecting cassava in the Americas

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Received: 14 July 2021 / Accepted: 24 October 2021 / Published online: 3 January 2022 © The Author(s) 2021

Abstract

We report the complete genome sequence of a field isolate of a novel bipartite secovirid infecting cassava in Colombia, provisionally named "cassava torrado-like virus" (CsTLV). The genome sequence was obtained using Oxford Nanopore Technology, and the 5' ends were confirmed by RACE. The RNA1 is 7252 nucleotides (nt) long, encoding a polyprotein of 2336 amino acids (aa) containing the typical "replication block", conserved torradovirus motifs, and a Maf/Ham1 domain, which is not commonly found in viral genomes. The RNA2 is 4469 nt long and contains two overlapping ORFs encoding proteins of 226 and 1179 aa, showing the characteristic genome arrangement of members of the genus *Torradovirus*.

Cassava torrado-like virus (CsTLV) is a partially characterized member of the family *Secoviridae* [1, 2] that was originally detected in cassava plants (*Manihot esculenta* Crantz) displaying root symptoms of cassava frogskin disease (CFSD) [3], an endemic disease of cassava in the Americas that can severely affect the root yield of the crop [4]. The virus is found in mixed infections [3, 5] and can induce leaf chlorotic spots symptoms in single infections in cassava [2]. Maf/HAM1 proteins are nucleoside triphosphate (NTP) pyrophosphatases that reduce mutagenesis by intercepting non-canonical NTPs and preventing their incorporation into DNA or RNA. They are highly conserved in prokaryotes and eukaryotes [6], but there are only a couple of examples of their presence in viral genomes [7, 8].

The complete genome of CsTLV was obtained from a cassava plant of the commercial variety Melua-31, collected in August 2020 in Yopal, Colombia, and total RNA extraction with CTAB was done as reported previously [9]. For library preparation, we followed the SQK-DCS109 protocol (Oxford Nanopore Technologies), which uses RNase

Handling Editor: Ralf Georg Dietzgen.

² AGROSAVIA, Centro de Investigacion La Libertad, Sede Yopal, Colombia Cocktail Enzyme Mix (Thermo Fisher) to eliminate ribosomal RNA. The library was loaded onto a FLO-MIN106 R9.4 flowcell and sequenced for 48 h in a MinION using MinKnow software v2.0. Basecalling was performed using Guppy v5.0.11, and assembly was performed as described by Leiva *et al.* [10]. The quality of the consensus sequence obtained was checked using Qualimap v2.2.1 [11], and lowcoverage regions and 5' ends were confirmed by sequencing of overlapping RT-PCR products and using a 5' RACE System for Rapid Amplification of cDNA Ends (Invitrogen).

Excluding the poly-A tail, the RNA1 (OK040225) is 7252 nt long and has a single open reading frame encoding a polyprotein of 2336 aa (260 kDa). It contains the typical "replication block" and a Maf/Ham1 domain at its 3' end at aa 2165 (Fig. 1A). The RNA2 (OK040226) is 4469 nt long and contains two ORFs: RNA2-ORF1 is 678 nt long and encodes a predicted protein of 226 aa (25 kDa). RNA2-ORF2 is 3534 nt long and overlaps with 44 nt of the 3' end of RNA2-ORF1; it encodes a predicted polyprotein of 1179 aa (131 kDa) containing the 3A/RNA2 movement protein domain (A3) and three coat proteins domains. The sequence obtained showed more than 98% aa sequence identity to all other partial CsTLV sequences available in the GenBank database, and BLASTp analysis revealed the highest aa sequence identity to squash chlorotic leaf spot virus (NC 035221; NC 035222), with 37.75% aa sequence identity and 82% coverage for RNA1 and 45.53% sequence aa identity and 77% coverage for RNA2.

Maf/Ham1 domains have only been reported in potyvirids. The first one was discovered by Mbanzibwa *et al.*

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Fig. 1 (A) Genome organization of CsTLV isolate Yop12 showing the location of conserved consensus motifs shared by torradoviruses [1] and the Maf/Ham1 domain (red frame). (B) Phylogenetic relationships of CsTLV to members of the genus *Torradovirus*, analyzed

using the aa sequences of RNA1 and RNA2 polyproteins. The phylogenetic tree was generated by the neighbor-joining method using MEGA. The evolutionary distances were computed using the Poisson correction method (number of aa substitutions per site).

[7] while working on the characterization of a Tanzanian isolate of cassava brown streak virus (genus *Ipomovirus*) (GenBank accession no. FJ039520.1), and a second one was reported by Knierim *et al.* [8] in a German isolate of euphorbia ringspot virus (genus *Potyvirus*) (GenBank accession no. NC_031339.1) (Fig. 2). Recently, Tomlinson *et al.* [12] demonstrated the activity of the potyvirid Maf/Ham1 in yeast and uncovered their role as a necrosis determinant in *Nicotiana benthamiana*, and James *et al.* [13] have suggested possible functions for this domain. In conclusion, CsTLV is

an atypical secovirid encoding a Maf/Ham1 protein domain, which has been described so far only in viruses infecting euphorbiaceous hosts [2, 7, 8]. Further studies are underway to determine the biological role of CsTLV Maf/Ham1 in the virus infection cycle in cassava.

| Α | * * * * | * * | * ** |
|---|--|--|--|
| CsTLV-Yop12 | SIQKFLIT <mark>TTN</mark> EG <mark>KKQE</mark> YIAQNQDKN | VLEFAKIETI <mark>EIQG</mark> -SVQ <mark>EI</mark> AVD <mark>K</mark> FRKVVKQV | /SDVRIVVS <mark>ED</mark> VSLEIDQCRLGPYV <mark>K</mark> FFSV |
| UCBSV-MLB3 | ALEDNDDSIEIN <mark>FVTGN</mark> KN <mark>K</mark> FA <mark>EV</mark> AA <mark>I</mark> TNGTGIV | /LVQTPLN <mark>LTE</mark> V <mark>QG</mark> -TRQ <mark>ET</mark> IMC <mark>K</mark> AKL <mark>A</mark> FQKI | LQT PVLVEDT <mark>SLELIGCNRMPGPYVK</mark> FFSN |
| CBSV-Tan_Z | TKDLRGREKLELRIESHDRTLQMQMKFPVT <mark>FVTGN</mark> LG <mark>K</mark> LA <mark>EV</mark> KS <mark>I</mark> LGIAND | DVMAKNI <mark>DL</mark> PEV <mark>QG</mark> -TPE <mark>EI</mark> VRK <mark>K</mark> AQL <mark>AVK</mark> M | TNSPVLVEDTCLCFNAFNGLPGPYIKWFLK |
| EuRSV-PV-0902 | VVDRPQSLNVAKREEEVTSKFRMGIEAPIT <mark>FVTGN</mark> AQ <mark>K</mark> LK <mark>EV</mark> KQ I FGPTIP | PIVSRKI <mark>DL</mark> PES <mark>QG</mark> -TVE <mark>ET</mark> IKE <mark>K</mark> ARVAAEL | /GGPVLVEDTSLCFDALNGLPGPYIKWFLE |
| Escherichia | MQKVVLA <mark>TGN</mark> VG <mark>KVRE</mark> LASLLSDFGLDIVA | AQTDLGV <mark>D</mark> SA <mark>E</mark> ET <mark>G</mark> LTFI <mark>E</mark> NAIL <mark>K</mark> ARH <mark>A</mark> AKV | TALPAIADDSGLAVDVLGGAPGIYSARYSG |
| Saccharomyces | MSNNEIV <mark>FVTGN</mark> AN <mark>K</mark> LK <mark>EV</mark> QS <mark>I</mark> LTQEVDNNNKTIH | ILINEAL <mark>DLEELQ</mark> DTDLNA <mark>I</mark> ALA <mark>K</mark> GKQ <mark>A</mark> VAAI | LGKGK <mark>PV</mark> F <mark>VEDT</mark> ALRFDEFN <mark>GLPGAYIK</mark> W <mark>F</mark> LK |
| Arabidopsis | MAAAAAKAAVVLPRPVT <mark>FVTGN</mark> AK <mark>K</mark> LE <mark>EV</mark> KA <mark>I</mark> IGNSIP | - FKSLKL <mark>DL</mark> P <mark>ELQG</mark> - EPED <mark>T</mark> SKE <mark>K</mark> ARL <mark>A</mark> ALQ' | /DGPVLVEDTCLCFNALKGLPGPYIKWFLE |
| Ното | KFPRT | ſĹVAQKI <mark>DĽ</mark> P <mark>E</mark> Y <mark>QG</mark> -EPD <mark>EI</mark> SIQ <mark>K</mark> CQE <mark>A</mark> VRQ | /QG PV L <mark>VEDT</mark> CLCFNALG <mark>GLPGPY</mark> I <mark>K</mark> WFLE |
| | | | |
| | | | |
| | * ** | * ** * * * ** | * * |
| CsTLV-Yop12 | * * SDFSGFVGRK <mark>A</mark> TLTLVQCVGS-TTSSTFSMQTKIIE <mark>G</mark> K <mark>I</mark> SEF | * ** * * * * ** P- <mark>Rg</mark> eng <mark>fgfd</mark> kv <mark>f</mark> eVegk <mark>t</mark> l <mark>aem</mark> tseg | * * KYSFGLRKITAHELGSVVSY |
| CsTLV-Yop12 UCBSV-MLB3 | * * SDFSGFVGRK <mark>A</mark> TLTLVQCVGS-TTSSTFSMQTKIIEG <mark>KI</mark> SEF ETIIDMVTCSEKTAAQ <mark>A</mark> I <mark>C</mark> TFALYDGKTMEIVE <mark>G</mark> ISN <mark>GDIV</mark> YE | * ** * * * * * * ** P- <mark>76</mark> ENG <mark>FGFD</mark> KVFEVEGK <mark>TLAEM</mark> TSEG EE <mark>76</mark> HNG <mark>FGVD</mark> CT <mark>FQ-DKQTGKTYAEM</mark> SPLE | * * KYSFGLRKITAHELGSVVSY ⁻ KNQV <mark>SHR</mark> AA <mark>AL</mark> KRLQEVLRRKGETQTEVRHQ |
| CsTLV-Yop12 UCBSV-MLB3 CBSV-Tan_Z | * * SDFSGFVGRKATLTLVQCVGS-TTSSTFSMQTKIIEGKISEF ETIIDMVTCSEKTAAQAICTFALYDGKTMEIVEGISNGDIVYE ELGLDGVVKMLSAFGDKSAYALCTFAYVH-NESSDPIVFKGVVNGEIVPF | * ** * * * * * * * * P- <mark>RG</mark> ENG <mark>FGFDKVFEVEGKULAEMTSEG EERGHNGFGWDCIFQ-DKQTGKUYAEMSPLE P-<mark>RGNNGFGWD</mark>PIFK-PDGCGC<mark>UFAEM</mark>PSSI</mark> | * * KYSFGL <mark>R</mark> KITAHELGSVVSY KNQVSHRAA <mark>AL</mark> KRLQEVLRRKGETQTEVRHQ KNDF <mark>SHRRRAL</mark> EKVKLFLDNLMVKQEKNKAS |
| CsTLV-Yop12 UCBSV-MLB3 CBSV-Tan_Z EuRSV-PV-0902 | * * SDFSGFVGRKATLTLVQCVGS-TTSSTFSMQTKIIEGKISEF ETIIDMVTCSEKTAAQAICTFALYDGKTMEIVEGISNGDTVYE ELGLDGVVKMLSAFGDKSAYALCTFAYVH-NESSDPIVFKGVVNGEIVPF GIGLEGLYKLVEPYQNRMASALCVFAFVN-KVGDDPIIFKGVLRGEIVMF | * ** * * * * * * * * P- <mark>RGENGFGFDKVFEVEGKTLAEMTSEG</mark> EERGHNGFGWDCIFQ-DKQTGKTYAEMSPLE P-RGNNGFGWDPIFK-PDGCGCTFAEMPSSI P-RGPNSFGWDPIFQ-PLDWKRTFAEMTEE | * * KYSFGLRKITAHELGSVVSY KNQVSHRAAALKRLQEVLRRKGETQTEVRHQ KNDFSHRRRALEKVKLFLDNLMVKQEKNKAS KNMISHRFRALSLVRDFLKSSSYFSFAKGLD |
| CsTLV-Yop12 UCBSV-MLB3 CBSV-Tan_Z EuRSV-PV-0902 Escherichia | * SDFSGFVGRKATLTLVQCVGS-TTSSTFSMQTKIIEGKISEF ETIIDMVTCSEK-TAAQAICTFALYDGKTMEIVEGISNGDTVYE ELGLDGVVKMLSAFGDKSAYALCTFAYVH-NESDDIVFKGVVNGEIVPF GIGLEGLYKLVEPYQNRMASALCYFAFVN-KVGDDPIFKGVLRGEIVMF EDATDQKNLQKLLETMKDVPDQRQAHFHCVLVVLRHAEDPTPLVCHGSWPGVITRE | * ** * * * * * * * * P-RGENGFGFDKVFEVEGKTLAENTSEG ERGHNGFONDCIFQ-DKQTGKTYAENSPL P-RGNNGFONDPIFQ-PLONKRTFAEMTEE PRGPNSFONDPIFQ-PLONKRTFAEMTEE EPAGTGGFGYDPIFF-VPSEGKTAAELTREE | * * KYSFGLRKITAHELGSVVSY KNQVSHRAAALKKRLQEVLRKKGETQTEVRHQ KNDFSHRRALEKVKLFLDNLMVKQEKNKAS KNMISHRRALSVVRDFLKSSSYFSFAKGLD KSAISHRGQALKLLDALRNG |
| CsTLV-Yop12 UCBSV-MLB3 CBSV-Tan_Z EuRSV-PV-0902 Escherichia Saccharomyces | * ** SDFSGFVGRKATLTLVQCVGS-TTSSTFSMQTKIIEGKISEF ETIIDMVTCSEKTAQQAICTFALYDGKTMEIVEGISMGDIVYE EIGLDGVVKMLSAFGDKSAVALCTFAYUH-NESSDPIVFKGVVNGEIVPF GIGLEGLYKLVEPYQNRMASALCVFAFVN-KVGDDPIIFKGVLRGEIVMF EDATDQKNLQKLLETMKDVPDDQRQAHFHCVLVYLRHAEDPTPLVCHGSWPGVTRK SMGLEKIVKMLEPFENKNAEAVTICFADSRGEYHFFQGITRGKIVPS | * ** * * * * * * * * P-RGENGFGFDKVFEVEGKTLAENTSEG EERGHNGFONDCIFQ-DKQTGKTVAENSPLE P-RGNNGFONDFIFK-PDGCGCTFAENPSSI P-RGPNSFONDFIFQ-PLDWKRTFAENMTEE EPAGTGGFQPDFF-VPSEGKTAAELTREE S-RGPTTFGWDSIFEPFDSHGLTVAENSKDA | * * KYSFGLRKITAHELGSVVSY KNQVSHRAAALKRLQEVLRRKGETQTEVRHQ KNDFSHRRALEKVKLFLDNLMVKQEKNKAS KNMISHRFALSLVRDFLKSSSYFSFAKGLD KSAISHRGQALKLLLDALRNG KNAISHRGKAFAQFKEYLYQNDF |
| CsTLV-Yop12 UCBSV-MLB3 CBSV-Tan_Z EuRSV-PV-0902 Escherichia Saccharomyces Arabidopsis | * ** SDFSGFVGRKATLTLVQCVGS-TTSSTFSMQTKIIEGKISEF ETIIDMVTCSEKTAQQAICTFALYDGKTMEIVEGISNGDIVYE ELGLDGVVKMLSAFGDKSAVALCTFAYVH-NESSDPIVFKGVVNGETVPF GIGLEGLYKLVEPYQNRMASALCVFAFVN-KVGDDPIIFKGVLRGETVMF EDATDQKNLQKLLETMKDVPDDQRQAHFHCVLVYLRHAEDPTPLVCHGSWPGVTRE SMGLEKIVKMLEPFENKNAFAVTICFADSRGEYHFFQGITRGKIVPS KLGHEGLNNLMAYEDKSAVALCAFSFSR-GPGAEPLTFLGKTPGKIVA | * ** * * * * * * * * * * P-RGENGFGFDKVFEVEGKTLAEHTSEG EERGHNGFGWDCIFQ-DKQTGKTYAEHSPLE P-RGNNGFGWDPIFK-PDGCGCTFAEHPSEG P-RGPNSFGWDPIFQ-PLDWKRTFAEHMTEE EPAGTGGFGYDPIFF-VPSEGKTAAELTREE S-RGPTTFGWDSIFEPFDSHGLTYAEHSKDA A-RGPTDFGWDPVFQ-PDGYDQTYAEHAKEE | * * KYSFGLRKITAHELGSVVSY KNQVSHRAAALKRLQEVLRRKGETQTEVRHQ KNOFSHRRALEKVKLFLDNLMVKQEKNKAS KNMISHRFALSLVRDFLKSSSYFSFAKGLD KSAISHRGQALKLLLDALRNG KNAISHRGKAFAQFKEYLYQNDF KNXISHR9KS_ALVKSHFKEAGYVFQTDDGT |
| CsTLV-Yop12 UCBSV-MLB3 CBSV-Tan_Z EuRSV-PV-0902 Escherichia Saccharomyces Arabidopsis Homo | * ** SDFSGFVGRKATLTLVQCVGS-TTSSTFSMQTKIIEGKISEF ETIIDMVTCSEKTAQQAICTFALYDGKTMEIVEGISMGDIVYE ELGLDGVVKMLSAFGDKSAYALCTFAYVH-NESSDPIVFKGVVNGEIVPF GIGLEGLYKLVEPYQNRMASQLCVFAFVN-KVGDDPIFKGVLRGEIVMF EDATDQKNLQKLLETMKDVPDDQRQAHFHCVLVYLRHAEDPTPLVCHGSWPGVITRE SMGLEKIVKMLEPFENKNAEAVTICFADSRGEYHFFQGITRGKIVPF KLGHEGLNNLLMAYEDKSAYALCAFSFSR-GPGAEPLTFLGKTPGKIVPF KLKPEGLHQLLAGFEDKSAYALCTFALSTGDPSQPVRLFRGRTSGRIVAF | * ** * * * * * * * * ** P-RGENGFGFDKVFEVEGKTLAEHTSEG EERGHNGFGWDZIFQ-DKQTGKTYAEHSPLE P-RGNNGFGWDZIFK-PDGCGCTFAEHPSSI P-RGPNSFGWDZIFQ-PLDWKRTFAEHMTEE EPAGTGGFGYDZIFF-VPSEGKTAAELTREE S-RGPTTFGWDSIFEPFDSHGLTYAEHSKDA A-RGPTDFGWDZVFQ-PDGYDCTYAEHAKEE P-RGCQDFGWDPCFQ-PDGYECTYAEHPKAE | * * * KYSFGLRKITAHELGSVVSY KNQVSHRAAALKRLQEVLRRKGETQTEVRHQ KNOFSHRRALEKVKLFLDNLMVKQEKNKAS KNMISHRFALSLVRDFLKSSSYFSFAKGLD KSAISHRGQALKLLLDALRNG KNAISHRGAFAQFKEYLYQNDF KNISHRYKSLALVKSHFKEAGYVFQTDDGT KNAVSHRFRALLELQEYFGSLAA |

В



Fig.2 (A) Sequence alignment showing the conserved sites of Maf/Ham1 domains from different taxa. The figure was made using Mview [14]. (B) Phylogenetic relationships of the Maf/ Ham1 domain. Viruses (in red): EuRSV-PV-0902, YP 009305422; CBSV-Nampula, AYW01246; CBSV-Tan_Z, ACT78701; CBSV-Ug65, QGW67508; CBSV-CGCC-2017, QCR98745; UCBSV-Kikombe, ARQ80023; UCBSV-MLB3, ACM48176; UCBSV-Ug_23, CBA18486; UCBSV-Ke_125, ASG92173; CsTLV-Yop12, ??OK040225??; Escherichia 1K7K_A; Pseudomonas,

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00705-021-05325-2.

Acknowledgements We are grateful to all our colleagues from the Virology Lab and the Cassava Program of CIAT. Special thanks to Dr. Amparo Rosero from Agrosavia and Dr. Diana Lopez-Alvarez from Universidad Nacional de Colombia, Palmira, for supporting this work. This research was co-funded by the CGIAR Research Program on Roots, Tubers, and Bananas (CRP-RTB) (https://www.cgiar.org/funders).

Author contributions AML carried out nanopore sequencing and analysis. JJ, HS, and SP performed molecular diagnostics, 5'RACE, and

WP_011064019; Burkholderia, KHS13049; Azoarcus, CAL96580; Rhizobium, CAK05869; Saccharomyces, CAA89597; Aspergillus, XP_754075; Neurospora, XP_955963; Arabidopsis, NP_567410; Oryza, XP_015613001; Manihot, XP_021594792; Caenorhabditis, AAL14111; Tetrahymena, XP_977249; Acyrthosiphon, NP_001233079; Drosophila, EDV32196; Culex, XP_038111262; Tribolium, XP_974197; Xenopus, AAI10772; Danio, NP_001093456; Mus, EDL28288; Homo, AAK21848

field activities. WJC designed the research, supervised the work, and wrote the manuscript. All authors approved the manuscript.

Funding CGIAR Research Program on Roots, Tubers, and Bananas

Availability of data and material Sequence data have been submitted to the GenBank database.

Declarations

Conflict of interest The authors declare no conflict of interest.

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