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BRIEF REPORT

Biological and molecular characterization of bean bushy stunt virus, a novel bipartite begomovirus infecting common bean in northwestern Argentina

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Abstract

Common bean plants (*Phaseolus vulgaris* L.) showing different virus-like symptoms were collected in northwestern Argentina. Dot-blot hybridization tests showed that the begomoviruses bean golden mosaic virus and tomato yellow vein streak virus were the most prevalent, but they also revealed the presence of unknown begomoviruses. The complete genome sequence of one of these unknown begomoviruses was determined. Sequence analysis showed that the virus is a typical New World begomovirus, for which the name "bean bushy stunt virus" (BBSV) is proposed. Biological assays based on biolistic inoculations showed that BBSV induced leaf roll and stunting symptoms similar to those observed in the field-collected common bean sample.

Common bean (*Phaseolus vulgaris* L.) is the second most important leguminous crop after soybean (*Glycine max* L.) and is the most important legume grown worldwide for direct human consumption. In Argentina, common bean is cultivated mainly in the subtropical northwestern region (NW) (provinces of Tucumán, Salta, Jujuy, Santiago del Estero, and Catamarca).

Diseases cause severe losses (20–100%) of yield and quality of common bean crops worldwide. Begomoviruses cause the most important viral diseases of common bean crops in Latin America, affecting more than 14 countries [27]. Begomoviruses (genus *Begomovirus*, family *Geminiviridae*) are circular single-stranded DNA viruses that infect dicotyledonous plants and are packaged in twinned icosahedral particles that are 20 × 30 nm in size [6]. These viruses are transmitted in a persistent, circulative manner by whiteflies of the *Bemisia tabaci* (Gennadius) cryptic species complex (Hemiptera: Aleyrodidae) [33]. Begomoviruses have either a bipartite or a monopartite genome. Bipartite begomoviruses have two 2.5- to 2.7-kb genomic components, named DNA-A and DNA-B, whereas monopartite begomoviruses consist of a single component that is a homolog of DNA-A of bipartite viruses [25].

Begomoviruses display high diversity in Central and South America, and several economically important crops have been reported to be infected by members of this genus [18, 26]. To date, members of six species have been identified infecting common bean in Argentina: *Bean golden mosaic virus*, *Tomato yellow spot virus*, *Soybean blistering mosaic virus*, *Tomato mottle wrinkle virus*, *Sida golden mosaic Brazil virus*, and *Tomato yellow vein streak virus* [15, 20, 31]. Here, we describe a survey of begomoviruses previously detected in common bean crops in Argentina and report the characterization of a new bipartite begomovirus.

During the 2017 growing season, 170 common bean plants showing mottling, yellow mosaic, chlorosis, blistering, dwarfing, leaf roll, and stunting symptoms were collected from the NW region.

The presence and relative incidence of begomoviruses were tested by dot-blot hybridization using a general probe that detects most begomoviruses as described previously [20]. The positive samples were subsequently analyzed with specific probes for bean golden mosaic virus

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(BGMV), tomato yellow spot virus (ToYSV), soybean blistering mosaic virus (SbBMV), tomato mottle wrinkle virus (ToMoWrV), sida golden mosaic Brazil virus (SiGMBRV) and tomato yellow vein streak virus (ToYVSV). The results obtained using the general probe showed that 21.2% of the samples were infected with begomoviruses. All of these samples were collected in the north of Salta province. BGMV and ToYVSV showed the highest relative incidence (69.4% and 61.1%, respectively). ToYSV and SiGMBRV showed an incidence of 5.6% and 2.8%, respectively, while none of the samples tested positive for ToMoWrV or SbBMV. It should be noted that 61.1% of the samples had coinfections in which ToYVSV was present. The most common mixed infection was BGMV-ToYVSV, which was detected in 19 out of the 22 coinfected samples with coinfection.

On the other hand, 10 samples tested positive when the general probe was used but tested negative when specific probes were used. The DNA from these samples was amplified by rolling-circle amplification (RCA) using a TempliPhi Amplification Kit (GE Healthcare, USA). The RCA products were digested with the restriction enzymes ApaI, BamHI, ClaI, EcoRI, EcoRV, HindIII, KpnI, PstI, SacI, SalI, and SmaI. Products that yielded a single band of approximately 2.6 kb were ligated into the pBluescript KS(+) vector (Stratagene, USA) for subsequent cloning [24]. The DNA from three samples could not be digested with the any of the restriction enzymes used.

The clones that were obtained were subjected to high-quality DNA extractions using a Zyppy ™ Plasmid Miniprep Kit (Zymo Research Corporation, USA) and sequenced. The initial sequencing of the viral inserts was performed using the oligonucleotide primers M13F and M13R, and the sequence was completed using the "primer walking" method [28] with specific primers designed using the AmplifX 1.7.0 [11] program. The nucleotide sequences were analyzed using the Chromas lite 2.01 program, assembled using SeqManTM II, and compared with other begomovirus sequences using the BLASTn program (https://blast.ncbi.nlm.nih.gov/Blast.cgi?PAGE_TYPE=BlastSearch). Although the clones from samples P165, P168, and P180 did not react with the specific BGMV probe, they showed more than 95% sequence identity to the DNA-A component of various BGMV isolates. On the other hand, clones from samples P100, P169, and P177 yielded inconclusive results. A partial sequence analysis of clones from sample P179 (179 Hind III-1, 179 Hind III-7, and 179 Hind III-8), obtained by digestion of the RCA product with HindIII, showed that these three clones correspond to the DNA-A and DNA-B of a novel begomovirus. Sample P179 was collected from General Mosconi (Salta province) and showed leaf roll and stunting symptoms (Fig. 1A).

The DNA-A component (clone 179 Hind III-1), is 2572 nt in length (GenBank accession number MN414067), and the DNA-B component (clone 179 Hind III-8) is 2522 nt in length (GenBank accession number MN414068). Both DNA components have the conserved begomovirus nonanucleotide sequence (5'-TAATATT/AC-3') in the stem-loop structure that indicates the origin of the viral replication, and their genome organization is typical of New World bipartite begomoviruses. The DNA-A sequence has five ORFs, one in the viral sense (CP) and four in the complementary sense (Rep, TrAP, REn and AC4), whereas the DNA-B sequence has two ORFs, one in the viral sense (NSP) and one in the complementary sense (MP) (Table 1). The two genomic components share 95.8% sequence identity in the common region (CR, 120 nt), indicating that DNA-A and DNA-B are cognate sequences of the same virus.

Fig. 1 (A) Common bean sample P179 showing leaf roll and stunting symptoms. (B) Inoculated common bean cv. Alubia plant showing typical BBSV symptoms. (C) Left to right, leaf distortion and interveinal chlorosis in cultivar CR5 and leaf blistering in soybean

Comparisons using Sequence Demarcation Tool version 1.2 (SDT v1.2) with the MUSCLE alignment option [17] revealed that the DNA-A sequence was most similar to that of pepper leafroll virus (PepLRV) (GenBank accession number KC769819) and that the DNA-B sequence was most similar to that of melochia mosaic virus (MelMV) (GenBank

Table 1 Open reading frames of the DNA-A and DNA-B components of bean bushy stunt virus (BBSV)

Sense[a]	Gene[b]	Position	Length (nucleotides)	Length (amino acids)	Genomic component
V	CP (AV1)	162-911	750	249	A
C	Rep (AC1)	2439-1384	1056	351	A
C	TrAP (AC2)	1442-1053	390	129	A
C	REn (AC3)	1306-908	399	132	A
C	AC4	2282-1989	294	97	A
V	NSP (BV1)	326-1132	802	268	B
C	MP (BC1)	2079-1201	879	292	B

[a]V, virion sense; C, complementary sense

[b]The ORFs are coded according to the function of their protein products; CP, coat protein; Rep, replication-associated protein; TrAP, transcriptional activator protein; REn, replication enhancer protein; AC4, suppression of RNA silencing; NSP, nuclear shuttle protein; MP, movement protein

accession number KT201152) (84.65% and 72.04% nucleotide sequence identity, respectively). Thus, the highest DNA-A sequence identity was below the species demarcation threshold established by the ICTV for begomovirus species [6]. Therefore, the novel begomovirus associated with leaf roll and stunting symptoms is a member of a new species, and we propose the name "bean bushy stunt virus" (BBSV) for this virus.

Phylogenetic analysis was performed using MEGA X software [12] by comparing the sequences obtained with those of the most closely related begomoviruses and other begomoviruses from South America available in the GenBank database (www.ncbi.nlm.nih.gov). The phylogenetic analysis of DNA-A sequence placed BBSV in a strongly supported clade with PepLRV (Fig. 2A), whereas the DNA-B sequences placed the new virus in a clade with euphorbia yellow mosaic virus (EuYMV) (GenBank accession number FJ619508) (Fig. 2B). No evidence of recombination was found in the BBSV DNA-A or DNA-B component using RDP4 software [13].

To assess the infectivity of BBSV in common bean plants, DNA-A and DNA-B clones were isolated and precipitated onto tungsten particles [5]. Common bean plants of the cultivar Alubia were inoculated with aliquots of

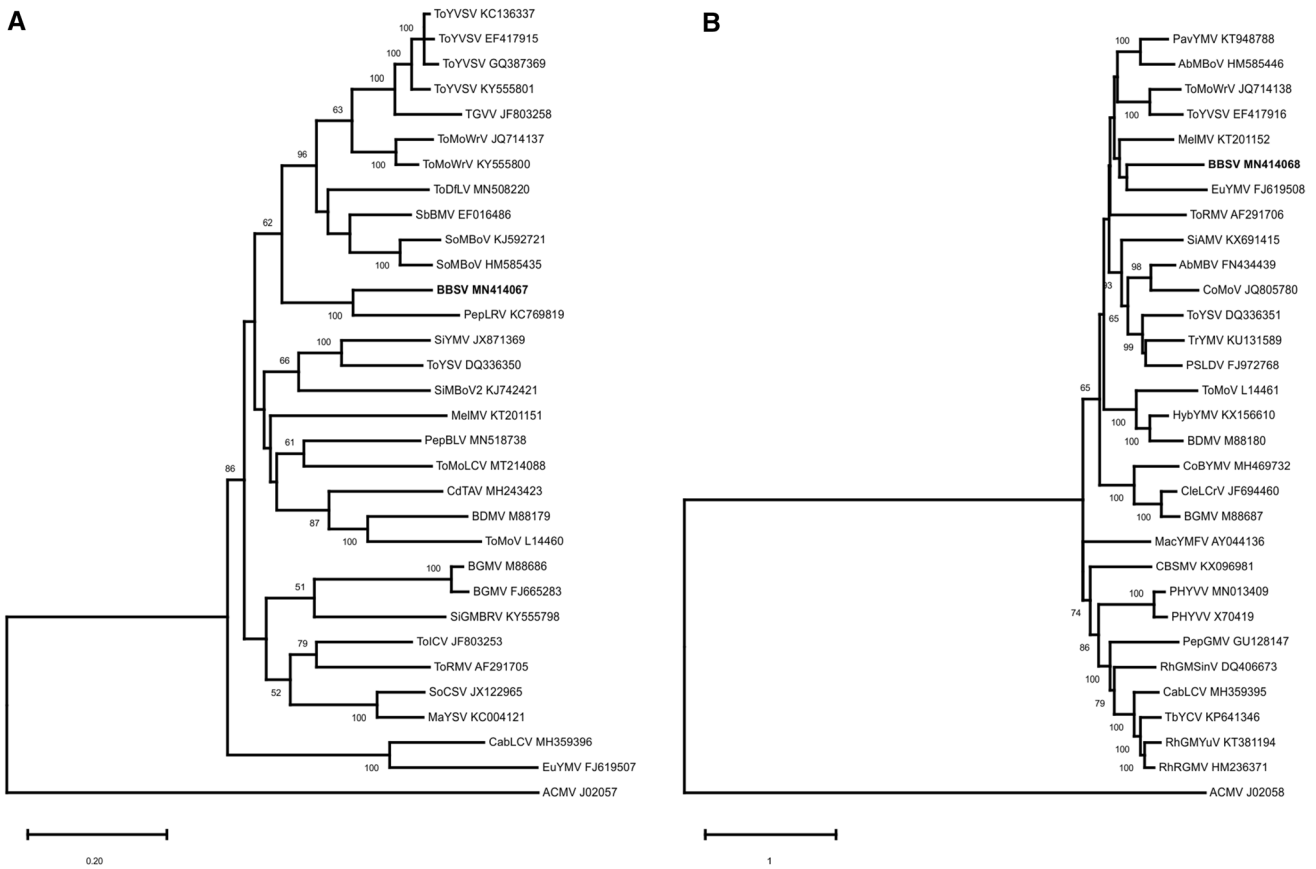

Fig. 2 Maximum-likelihood phylogenetic trees constructed using the complete nucleotide sequences of the DNA-A (A) and DNA-B (B) components of bean bushy stunt virus (BBSV) and the most closely related begomoviruses. Complete begomovirus names and GenBank accession numbers are listed in Supplementary Table 1. African cassava mosaic virus (ACMV) was used as an outgroup

8 µL of the precipitated DNA per plant using a biolistic particle delivery system at 650 or 1100 psi onto unifoliate leaves using a Bio-Rad PDS-1000/He system (Bio-Rad, USA). Regardless of the pressure used, all inoculated plants showed leaf roll, dwarfism, and stunting symptoms (Fig. 1B) similar to those observed in the field-collected sample. Moreover, when DNA of symptomatic plants was amplified by PCR using BSSV-specific primers (5'-GAA GTTCTTCGCGTTAACTGAG-3'/ 5'-GAGATAAGC CTTGTGGAGAGCCAAC-3'), a 1309-bp fragment was obtained.

The host range of the new virus was tested by inoculating the following species/cultivars: common bean cv. Alubia, NAG12 and CR5, tomato (*Solanum lycopersicum* L.), pepper (*Capsicum annuum* L.), soybean (*Glycine max* L.), and the weed *Leonurus sibiricus* L. The results indicated that this virus only induced symptoms in the common bean cultivars and soybean. The Alubia cultivar showed severely stunted growth and leaf curling, as was observed in the field plants. Cultivars NAG 12 and CR5 were able to develop a larger number of leaves; however, they showed marked blistering, leaf distortion, interveinal chlorosis, and reduced growth, whereas the soybean plants showed leaf blistering and stunted growth (Fig. 1C). In all cases, infection was confirmed by PCR with BBSV-specific primers.

A specific probe for BBSV was generated using primers (5'-CTTATACTGGCCCACAACTAACTG-3'/5'-TAAGCG GGATGCCCCAT-3') that amplify the common region. The PCR product (165 bp) was labeled with digoxigenin using a DIG DNA Labeling and Detection Kit (Roche Applied Sciences, Indianapolis, USA). The probe specificity was tested by dot-blot hybridization, and it was found to react only with its homologous viral targets. No cross-reaction was observed with other begomoviruses or the negative control. Next, samples that tested positive with the general probe were analyzed with the new BBSV probe. The results showed that only two of the 36 begomovirus-positive samples reacted with the BBSV-specific probe (incidence, 5.6%). One of them was the original P179 sample, and the other was sample P178. Both samples were collected from the same field in General Mosconi (Salta province) and had the same symptoms. In addition, sample P178 also reacted with the ToYVSV probe.

In Argentina, the first begomovirus outbreak was observed in the 1980s, and this was a consequence of the expansion of soybean and cotton crops [16]. In addition, the presence of an important cryptic whitefly species (the begomovirus vector), such as New World 2 (NW2), and two introduced species, Middle East-Asia Minor 1 (MEAM1) and Mediterranean, was confirmed in common bean crops in northern Argentina [3]. Thus, it is common to observe the presence of begomoviruses in common beans, near crops and weeds.

Detection tests for BGMV, ToYSV, SbBMV, ToMoWrV, ToYVSV, and SiGMBRV, based on DNA hybridization probes have demonstrated the constant presence of these viruses in the NW region [20, 22, 31]. In Salta province, as presented in this work, the high proportion of positive samples (100%) and the large diversity of begomoviruses, as well as the high frequency of coinfections, are likely to favor emergence of new viruses through processes such as recombination or pseudo-recombination [5, 23]. The use of specific detection probes can help us to demonstrate the presence of previously reported begomoviruses or to provide clues regarding the presence of still unknown viruses. However, false negatives can also occur, as we unexpectedly observed with three samples corresponding to BGMV isolates that could not be detected using the specific probe, probably due to the poor quality of the extracted DNA or a low viral titer [1]. On the other hand, only 21.2% of the symptomatic common bean samples were infected with begomoviruses; therefore, the remaining samples could have been infected by other viruses [1, 19] or affected by herbicides [21]. In this work, we detected and characterized BBSV, a new begomovirus infecting common bean crops in Argentina. Although BBSV was detected at low incidence, this is the first time it has been studied, and only common bean samples were tested. It would be advisable to extend the detection tests to other alternative hosts and other regions, especially considering the severity of its symptoms.

It should be noted that the BBSV DNA-A genomic component has the highest sequence identity to that of PepLRV, a begomovirus that was detected in Peru infecting chili pepper and causes similar leaf roll symptoms. It has also been observed in common beans, with high incidence values, and infecting wild plants such as *Nicandra physaloides* [14]. Also, a novel strain of PepLRV was reported in Ecuador infecting common bean and soybean [9]. In addition, other begomoviruses were phylogenetically grouped with BBSV and PepLRV, including ToMoWrV, a begomovirus that is a recombinant between ToYVSV and SbBMV and was detected in tomato [30]. ToYVSV has also been reported in tomato and potato in Brazil [2], and SbBMV has been reported to infect common bean, soybean, and tomato in Argentina [20]. All of these viruses have been reported in Argentina infecting common bean [31]. On the other hand, the BBSV DNA-B genomic component has the highest sequence identity to MelMV, a begomovirus isolated from the weed *Melochia* sp. from Brazil. This plant, a common weed in South America, often grows near economically important crops [10]. Another phylogenetically related begomovirus, euphorbia yellow mosaic virus (EuYMV), was also isolated from a weed, *Euphorbia heterophylla* [7].

The biolistic inoculation tests allowed us to conclude that the host range of BBSV is limited to leguminous species, although some of the other viruses detected in common

bean in Argentina, such as SbBMV, ToYSV, ToYVSV, and ToMoWrV, have a broader host range that includes members of the family Solanaceae [6, 31]. The restricted host range of BBSV might limit its ability to evolve rapidly and cause greater economic losses. However, results from inoculation experiments do not always correspond to situations where the virus is transmitted naturally by the whitefly *Bemisia tabaci* (Gennadius), in which case the expression of symptoms and the range of hosts can vary. Moreover, considering the phylogenetic relationships of BBSV and its genetic resemblance to begomoviruses isolated from weeds such as *Melochia* sp. [10], *N. physaloides* [14], and *Euphorbia heterophylla* [7, 32], it is necessary to carry out the assay on not only plants of economic value but also on weeds, since they can constitute the reservoirs and primary sources of inoculum for this pathogen [4, 5, 8, 29].

It should be noted that soybean and common bean crops are cultivated in the same production area in northern Argentina, but at different times, with the soybean maturity stage coinciding with sowing and onset of growth of common bean; thus, the latter crop becomes more palatable for different pests, such as whitefly. For these reasons, it is possible to expect the development of new begomovirus outbreaks.

The great variability of begomoviruses, their ability to evolve, their relationship with the vector, and the presence of alternative hosts favor the emergence of new viruses that can cause major damage to crops. Knowledge of these new viruses and their molecular and biological characteristics is necessary for the development of disease control and management strategies.

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Compliance with ethical standards

Conflict of interest There is no conflict of interest.

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