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Research Article

Molecular Detection and Phylogenetic Characterization of Soybean Mosaic Virus Infecting Soybean (*Glycine max* L.)

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ABSTRACT

Soybean (*Glycine max* L.) is one of the world's most important legume crops, valued for its high protein content and extensive applications in food, feed, and industrial products. However, soybean production is frequently threatened by Soybean mosaic virus (SMV), one of the most destructive viral pathogens affecting crop yield and seed quality. This study aimed to detect and molecularly characterize SMV infecting soybean in Uzbekistan. During the 2023 growing season, leaf samples were collected from 35 soybean varieties exhibiting typical virus-like symptoms, including mosaic, yellowing, stunting, and leaf deformation, from the experimental field of the Institute of Genetics and Experimental Plant Biology of the Republic of Uzbekistan. Total RNA was extracted from symptomatic plants and subjected to RT-PCR using SMV-specific primers targeting the coat protein (CP) gene. A DNA fragment of approximately 756 bp was successfully amplified from infected samples, confirming the presence of SMV. The amplified CP gene was sequenced and analyzed to determine its genetic relationship with previously reported SMV isolates. Phylogenetic analysis showed that the Uzbek isolate TH-UZB1 (GenBank accession no. OQ385206.1) clustered closely with Korean SMV isolates and shared high nucleotide identity with the Serbian isolate NDS_21, indicating a high degree of genetic similarity. The molecular detection and characterization of SMV reported in this study provide valuable information on the occurrence and genetic identity of the virus in Uzbekistan. These findings contribute to a better understanding of the genetic diversity of SMV and provide a scientific basis for disease surveillance, resistance breeding, and the development of effective management strategies for sustainable soybean production.

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1. INTRODUCTION

Soybean (*Glycine max* L.) is a self-pollinated annual legume of the family Fabaceae and one of the principal sources of vegetable oil and high-quality plant protein. Its expanding cultivation also contributes to crop diversification and food security. In Uzbekistan, soybean production has received increasing attention within national agricultural development efforts (Ministry of Agriculture of the Republic of Uzbekistan, 2023).

Soybean production is threatened by more than 100 reported viruses, among which Soybean mosaic virus (SMV), a member of the genus Potyvirus, is one of the most widespread and economically important. Depending on cultivar susceptibility, virus strain, infection timing, and environmental conditions, SMV can cause substantial yield and seed-quality losses (Hill & Whitham, 2014; Hajimorad et al., 2017). The virus is transmitted through infected seed and non-persistently by numerous aphid species, including Aphis glycines. Infected plants may develop mosaic, mottling, leaf deformation, stunting, and seed-coat mottling; however, symptom expression varies with the host genotype and growing conditions (Liu et al., 2016; Fang et al., 2024). At the molecular level, SMV possesses a single-stranded, positive-sense RNA genome that is translated as a polyprotein and subsequently processed into functional viral proteins. Sequence variation within this genome provides a basis for distinguishing isolates and examining their evolutionary relationships (Hajimorad et al., 2017). Because visual symptoms may overlap with those caused by other pathogens or abiotic stress, molecular detection and sequence analysis are needed for reliable identification and genetic comparison of field isolates (Elmore et al., 2022).

Despite the growing importance of soybean cultivation in Uzbekistan, peer-reviewed molecular information on SMV occurrence and genetic variation in the country remains limited. This information gap restricts evidence-based assessment of local virus populations and complicates the selection of appropriate material for resistance breeding. Characterization of local isolates is therefore necessary to establish an epidemiological baseline and to support surveillance, the use of virus-free seed, and resistance-breeding programmes. The P1 region of the SMV genome provides sequence variation useful for comparing isolates and assessing their phylogenetic relationships (Hajimorad et al., 2017; Liu et al., 2016).

Therefore, this study aimed to detect SMV in symptomatic soybean plants cultivated in Uzbekistan by RT-PCR, characterize the amplified P1 gene fragment, and determine the phylogenetic position of the Uzbek isolate relative to reference isolates deposited in GenBank. The results provide molecular evidence of SMV in Uzbek soybean and a basis for subsequent studies of its distribution, diversity, and management.

2. METHODOLOGY

2.1. Survey Areas and Sampling

To detect SMV, the causal agent of soybean mosaic disease, leaf samples were collected from 35 soybean varieties and breeding lines exhibiting typical virus-like symptoms, including mosaic, yellowing, stunting, and leaf deformation. Sampling was conducted during the 2023 growing season at the experimental field of the Institute of Genetics and Experimental Plant Biology of the Republic of Uzbekistan. A total of three leaf samples were collected, with three biological replicates per variety/line; of these samples were subsequently confirmed SMV-positive by RT-PCR, corresponding to an overall infection rate of 100 %. The collected leaves were placed in labelled plastic bags and stored at −80°C until further analysis to preserve the integrity of the viral RNA.

2.2. Determination of the Degree of Disease

To determine the degree of disease, 20 plots of 1 m^2 were marked along two diagonally intersecting lines within a 1-ha areaplants within each plot were examined and scored according to the method of Vlasov, as cited in Liu et al. (2016), using the following formula:

$$P = \frac{n \times 100}{N}$$

where P is the disease level of the plants (%), n is the number of infected plants, and N is the total number of plants examined.

2.3. Inoculation, Virus Purification, and Growth-Chamber Transfer

Inoculum was prepared from symptomatic leaves homogenized in 0.02 M phosphate buffer (pH 7.4) and mechanically inoculated onto carborundum-dusted leaves following standard procedures (Foster et al., 2007; Hull, 2014). Inoculated plants were kept under cool, low-light conditions for 1-2 h, labelled, and monitored for symptom development.

2.4. Extraction and Purification of Total RNA

Leaf samples (0.1 g) were ground to a fine powder in liquid nitrogen, and total RNA was extracted using the Invitrogen PureLink RNA Mini Kit according to the manufacturer's protocol. RNA integrity was verified by 1% agarose gel electrophoresis, and purity and concentration were measured spectrophotometrically. RNA samples were stored at −80°C until further processing.

2.5. Synthesis of Complementary DNA (cDNA)

Complementary DNA (cDNA) was synthesized using SuperScript IV Reverse Transcriptase in a final reaction volume of 20 µL. Total RNA (5 µL) was mixed with reverse primer Lu4, 2.5 mM dNTPs, and nuclease-free water, incubated at 65°C for 5 min, then chilled on ice for 3 min before adding 5× buffer, 0.1 M DTT, and reverse transcriptase. Reactions were incubated for 1 h 55 min at 41°C in a T960 PCR Thermal Cycler, followed by 10 min at 70°C to inactivate the enzyme.

2.6. Amplification by PCR

PCR amplification was performed in a 25 µL reaction containing 10× PCR buffer, 2.5 mM dNTP mix, 25 mM $MgCl_2$, forward and reverse primers (SMV-P1-F and SMV-P1-R, 10 pM each), Taq DNA Polymerase (5 U/µL), and synthesized cDNA template. Thermal cycling (Sambrook & Russell, 2001) comprised initial denaturation at 94°C for 3 min; 35 cycles of 94°C for 30 s, 55°C for 45 s, and 72°C for 1 min; and a final extension at 72°C for 7 min. Sequence-verified SMV-positive cDNA served as the positive control and nuclease-free water as the negative control.

2.7. Agarose Gel Electrophoresis

The amplification products were analyzed by electrophoresis on a 1.5% (w/v) agarose gel prepared in 1× TAE (Tris-Acetate-EDTA) buffer and stained with ethidium bromide (0.5 µg/ml) or an alternative nucleic acid gel stain. Electrophoresed gels were visualized and documented under ultraviolet (UV) transillumination using a gel documentation system to confirm the presence and size of the expected 756 bp target fragments.

2.8. Statistical Analysis

Data from the biological characterization assays (dilution end-point and thermal inactivation) were obtained from three independent biological replicates and are expressed as mean ± standard deviation. Field disease-incidence data are reported as descriptive counts and percentages based on visual symptom scoring (Vlasov method) across the 20 sampled plots per field and were not subjected to formal hypothesis testing, as plot-level replicate data were not analyzed statistically in this study.

3. RESULTS AND DISCUSSION

In September 2023, a large-scale survey was conducted at the experimental field of the Institute of Genetics and Experimental Plant Biology of the Republic of Uzbekistan (Figure 1). The institute maintains a collection of more than 90 soybean varieties and breeding lines, with seed stocks renewed annually. Current breeding efforts focus on developing phytopathogen-resistant soybean varieties adapted to local climatic conditions for cultivation across Uzbekistan.

The phytosanitary status of the field was assessed mainly during the first and second stages of soybean development. Disease symptoms were more pronounced during the second stage. A total of 35 soybean varieties and breeding lines showing virus-like symptoms were selected for further analysis (Table 1). The observed symptoms included mosaic, chlorosis, necrotic leaf spots, deformation of plant organs, stunted growth, and wilting. The severity of viral infection was evaluated using the Vlasov method based on visual symptoms (Figure 2).

Figure 1. Soybean fields of the Institute of Genetics and Experimental Plant Biology of the Republic of Uzbekistan.

Figure 2. Representative images of soybean leaves exhibiting vein-associated chlorosis under field conditions.

Table 1. Distribution of SMV among soybean varieties and lines.

No.	Name of variety / line	Total tested plants	Infected plants	Total degree of disease, %
1	Amigo	100	-	-
2	Selection 302	80	-	-
3	Gavhar	250	-	-
4	Oyjamol	240	-	-
5	Vilona	180	4	2.2
6	Productive	140	4	2.8
7	Slovenia	150	-	-
8	A blessing	190	-	-
9	Victoria	160	-	-
10	Tomaris	200	-	-
11	Gene 1	120	60	50
12	Gene 2	100	12	12
13	Gene 3	101	15	15
14	Gene 4	90	8	9
15	Gene 5	95	6	6.5
16	Gene 6	85	4	5
17	Gene 7	100	5	5
18	Gene 8	100	7	7
19	Gene 9	80	6	7.5
20	Gene 10	70	9	13
21	Gene 11	65	-	-
22	Gene 12	60	3	5
23	Gene 13	62	-	-
24	Gene 14	68	4	6
25	Gene 15	64	3	5
26	Gene 16	62	-	-
27	Gene 17	65	-	-
28	Gene 18	69	-	-
29	Gene 19	72	13	18
30	Gene 20	58	6	10.5
31	Gene 21	56	-	-
32	Gene 28	62	14	23
33	Gene 33	62	12	20
34	Gene 34	76	26	34
35	Andijan	78	6	8

Based on the distribution of SMV among varieties and lines planted in the experimental field, monitoring showed that lines Gene 1, Gene 2, Gene 3, Gene 19, and Gene 34 exhibited a moderate level of disease. Varieties and lines such as Vilona, Productive, Gene 6, Gene 7, Gene 12, Gene 14, and Andijan, together with the remaining varieties and lines that showed a low disease level, appeared to be more resistant to SMV. A chi-square test of independence confirmed that infection incidence differed significantly among varieties/lines ($\chi^2(34) = 705.22$, $p < 0.001$, n = 3,610 plants pooled across two replicate field plots per variety/line, 227 infected), consistent with the wide range of disease levels observed, from no detectable infection in varieties such as Amigo, Selection 302, Gavhar, and Oyjamol to 50% incidence in Gene 1. Samples from symptomatic plants (leaves) were collected, and the degree of infection was determined in the laboratory. The viral samples were mechanically inoculated to assess infectivity, and results showed an increase in the level of virus infection. In previous experiments, the first sample taken from a plant displaying mosaic symptoms produced mottling and puckering on *Chenopodium amaranticolor* and *Vigna unguiculata* (Figure 3), as well as necrotic spots and systemic mosaic symptoms on *Datura stramonium*, *Nicotiana tabacum* and *Chenopodium quinoa*.

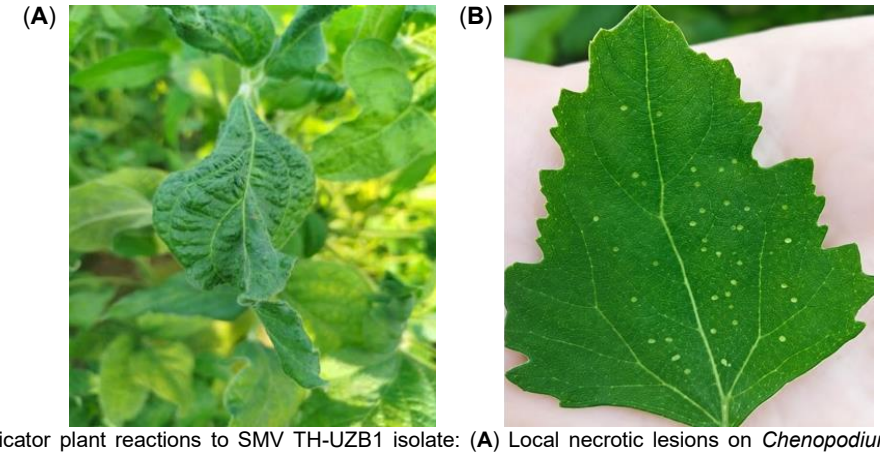

Figure 3. Indicator plant reactions to SMV TH-UZB1 isolate: (**A**) Local necrotic lesions on *Chenopodium amaranticolor*. (**B**) Systemic mosaic, mottling, and vein necrosis on *Nicotiana tabacum*, confirming SMV pathogenicity.

Several tests can be used to study the physical and molecular characteristics of SMV isolates, including virus isolation using indicator plants, virus purification, complete identification, evaluation of appropriate methods, and application of modern molecular techniques such as RT-PCR and PCR. In this study, RT-PCR was used to amplify a partial sequence of the CP gene in soybean samples, generating a 756-bp fragment (Figure 4) of the coat-protein region of the SMV isolates using the SMV-P1-F forward primer and the SMV-P1-R reverse primer (Table 2).

Table 2. Primer set used for identifying SMV in this study.

Target region	Primer name	Sequence (5'-3')	Product size (bp)
P1	SMV-P1-F	GCATGGCGATTTCTGTGCC	756
P1	SMV-P1-R	CAAACAGTAAACCACTATCTC	

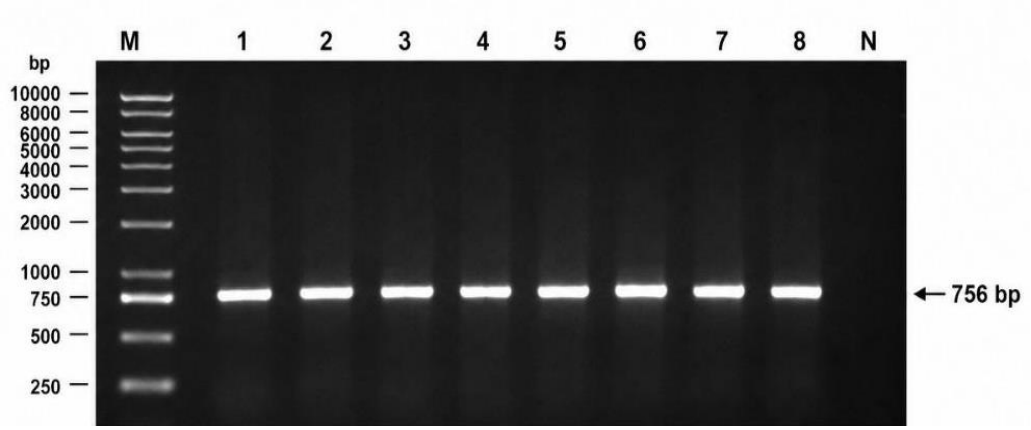

Figure 4. RT-PCR detection of Soybean mosaic virus (SMV) using SMV-P1-F/SMV-P1-R primer pair. Agarose gel electrophoresis (1%, w/v) of RT-PCR products showing a 756 bp amplicon. Lane M: 100 bp DNA ladder; Lanes 1-8: RT-PCR products from eight symptomatic soybean samples selected on the basis of visible disease symptoms; Lane N: negative control (asymptomatic, healthy soybean plant). The consistent presence of the expected 756 bp fragment in Lanes 1-8, and its absence in Lane N, confirms successful molecular detection of SMV in field-collected symptomatic samples.

Sequence data were analyzed using MEGA X software and compared with reference isolates to construct a phylogenetic tree. Partial coat-protein sequences were successfully obtained from all eight SMV-positive samples collected in the experimental field. To compare the Uzbekistan SMV isolates (trimmed length: 756 bp) with isolates reported from other regions worldwide, phylogenetic analyses were conducted using reference sequences deposited in GenBank. The molecular characteristics of the Uzbekistan SMV isolates are illustrated in Figure 5. BLAST analysis against the NCBI database confirmed that the sequences examined corresponded to the SMV serotype. Specifically, BLAST analysis revealed that isolate TH-UZB1 (accession no. OQ385206.1) shared 99-100% nucleotide sequence identity with SMV isolates from other countries, including the highest similarity (100%) with the Korean isolate (AJ290450.1), SMV partial P1 gene isolate CN7 (AJ639653.1), and isolate CN31 (AJ639647.1).

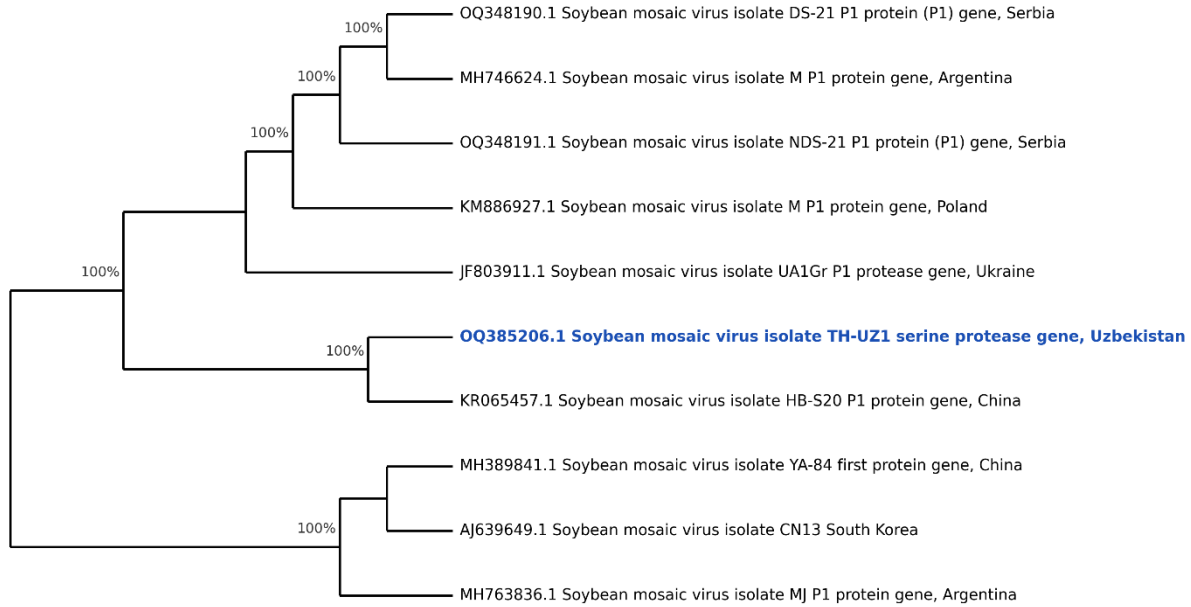

Figure 5. Phylogenetic relationships of the Soybean mosaic virus TH-UZB1 isolate (GenBank accession OQ385206.1) from Uzbekistan. Neighbour-joining tree constructed from P1 gene sequences (756 bp) using the Kimura 2-parameter substitution model with 1000 bootstrap replicates. Bootstrap support values (shown only when ≥ 50%) are displayed above each branch node. The TH-UZB1 isolate clusters within a clade comprising Korean SMV strains and shares 98-100% nucleotide identity with reference isolates from Korea (AJ290450.1), China (AJ639653.1, AJ639647.1), and Serbia (OQ348191.1), indicating broad geographical distribution and genetic conservation of the P1 gene region.

For phylogenetic analysis, the partial CP gene sequence of the Uzbekistan isolate TH-UZB1 (OQ385206.1) was compared with 11 homologous SMV strains available in GenBank. According to the resulting phylogenetic tree, the TH-UZB1 sequence clustered with seven Korean isolates (AJ290450.1) and with an isolate associated with the emergence of RSV-resistance-breaking SMV in Korean soybean cultivars (AJ639652.1). Phylogenetic analysis and multiple sequence alignment (ClustalW) indicated that four mutation events (133G>A, 223T>C, 323G>A) distinguish the TH-UZB1 isolate from the SMV NDS_21 isolate from Serbia, and appear to have contributed to the evolutionary divergence of the Uzbekistan (TH-UZB1) haplotype (Figure 6).

Comparative analysis of the TH-UZB1 isolate with the deduced coat protein of the Serbian isolate SMV NDS_21 showed that the three substitutions 133G>A, 223T>C, and 323G>A in TH-UZB1 were missense mutations resulting in amino acid substitutions. Specifically, these nucleotide changes correspond to Asp→Asn, Ile→Thr, and Val→Met substitutions in the deduced P1 protein sequence. Although these residues lie outside the core catalytic domain of the P1 protease, substitutions at surface-exposed positions of potyviral P1 proteins have been associated with altered protein–protein interactions during genome amplification and can modulate aphid transmission efficiency or host-range specificity in related potyviruses (Cui et al., 2011; Rehman et al., 2021). Whether these specific substitutions confer a functional advantage to the TH-UZB1 isolate remains to be experimentally verified. SMV is widespread globally and infects cultivated and wild plant species belonging to the Fabaceae, Amaranthaceae, Chenopodiaceae, Passifloraceae, Scrophulariaceae, and Solanaceae families; it also causes yield losses in other crops such as barley, wheat, and sorghum (Cui et al., 2011). Phylogenetic analysis of the TH-UZB1 isolate revealed both similarities and differences relative to other strains worldwide. The tree shows that isolate TH-UZB1 (OQ385206.1), isolated from soybean at the Institute

of Genetics and Experimental Plant Biology of the Republic of Uzbekistan, shares 98.99% similarity with the Serbian SMV NDS_21 isolate (OQ348191.1).

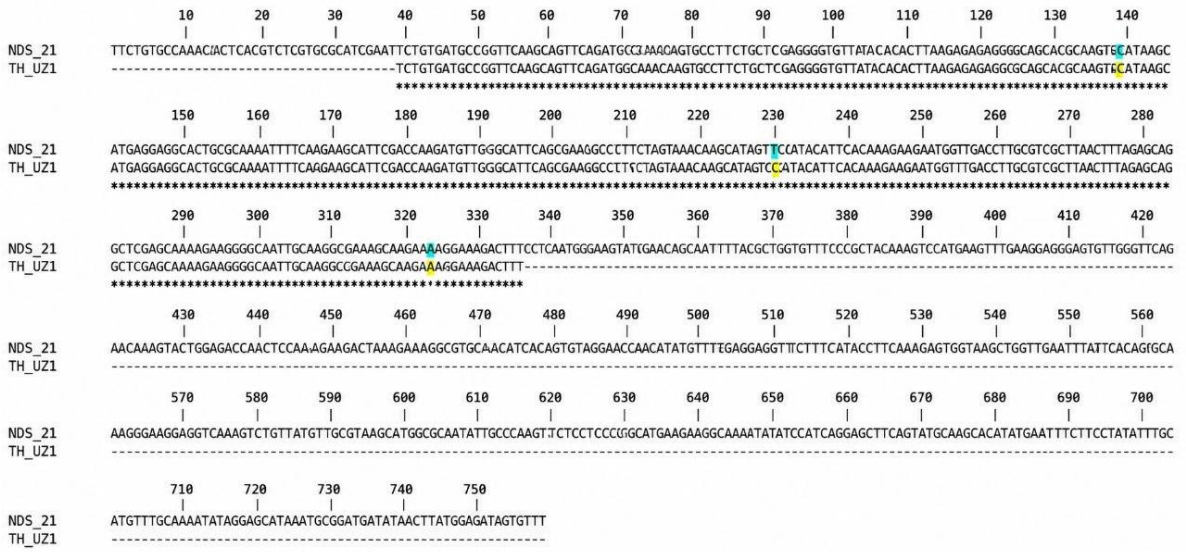

Figure 6. Multiple sequence alignment of the P1 gene coat protein region comparing the SMV TH-UZB1 isolate (Uzbekistan) with the SMV NDS_21 isolate (Serbia). Alignment generated using ClustalW. Asterisks (*) indicate identical residues; colons (:) and periods (.) denote conserved and semi-conserved substitutions, respectively. Boxed regions highlight the four nucleotide positions (133G>A, 223T>C, 323G>A, and one additional site) where TH-UZB1 differs from NDS_21. These substitutions result in three amino acid changes in the P1 protein (Asp→Asn, Ile→Thr, Val→Met) that may influence viral transmissibility or host recognition..

To investigate certain physical properties of SMV isolates, sensitivity screening of the virus was performed in a soybean field near the Institute of Genetics and Experimental Plant Biology of the Republic of Uzbekistan. To test SMV sensitivity, a crude leaf extract from SMV-infected soybean plants was serially diluted (10^{-1}, 10^{-2}, 10^{-3}, and 10^{-4}), and 100 µL of each dilution was applied to the sample pad of the test strip; the final dilution at which SMV remained detectable was 10^{-4}. Crude leaf extracts were then heated sequentially at 10, 20, 30, 40, 50, 60, 70, and 80°C for 10 min at each temperature, using a crude extract from SMV-free soybean leaves as a negative control. Loss of activity of the circulating SMV isolate was observed at 70°C (Figure 7).

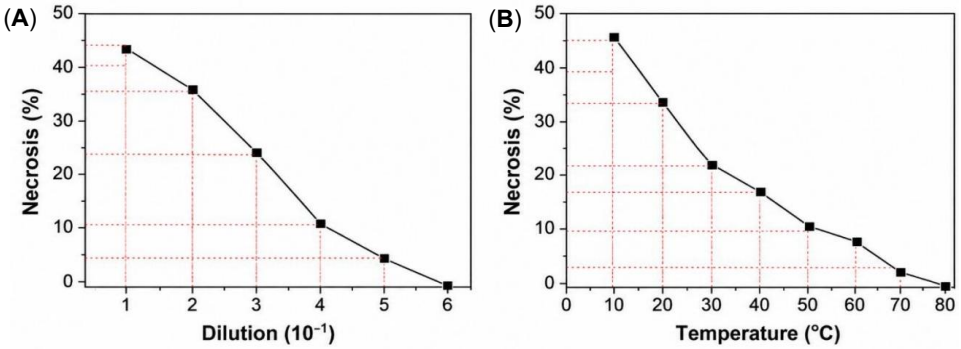

Figure 7. Biological properties of SMV TH-UZB1 isolate. (**A**) Dilution end-point assay showing infectious titer remains detectable at 10^{-4} dilution on Chenopodium quinoa. (**B**) Thermal inactivation curve indicating complete loss of infectivity at 70°C. Each point represents mean ± SD from three independent replicates.

SMV is among the most prevalent viruses affecting soybean worldwide, causing yield reductions ranging from 8% to 35%, with reported losses reaching up to 94% (Hill, 1999; Wang et al., 2005) that can reach substantial levels under natural field conditions. Infection by SMV, which spreads through aphids and seed transmission, can significantly decrease both seed production and quality. Seed-borne transmission of SMV is relatively low (around 5%) in most commercially available cultivars. Using pathogen-free seed can help prevent introduction of the virus into disease-free fields. While no SMV-resistant soybean varieties are currently available in Uzbekistan, some cultivars show reduced sensitivity to the virus. Control of virus spread through aphid management has proven inconsistent and unreliable. Alternative biological control approaches, such as Bacillus-derived antiviral ribonucleases and *Bacillus subtilis*- or *Bacillus velezensis*-based biocontrol agents effective against phytopathogenic fungi, may offer additional tools for managing plant viruses such as SMV in the future (Narmukhamedova

et al., 2024, 2025). Aphid species such as Aphis fabae, Aphis glycines, and Myzus persicae are responsible for the secondary, non-persistent spread of SMV. In North America, seed-borne infection is the primary source of SMV inoculum, and host resistance to seed transmission can limit the availability of inoculum sources (Liu et al., 2016).

Fifty-two ancestral North American soybean lines were evaluated for resistance to Bean pod mottle virus, SMV strains G1 and G5, Tobacco ringspot virus, and Tobacco streak virus. However, many cultivar-registration reports did not include reactions to SMV; the relatively high frequency of SMV resistance among major ancestral lines suggests that SMV resistance in U.S. cultivars may be more common than previously thought (Wang et al., 2005). The resistance or susceptibility of most commercial soybean cultivars to SMV remains unknown. In 2000, the soybean aphid, Aphis glycines, native to Asia, was found colonizing soybean plants in the Midwestern United States; it has since spread across all soybean-producing areas in North America and become a major threat to production. The aphid reduces yield directly by colonizing plants and diverting photosynthates away from seed production, and indirectly by spreading viral diseases such as SMV. Large outbreaks of the soybean aphid, particularly in 2003, caused significant economic impacts, with producers spending millions on registered insecticides to mitigate yield losses (Yao et al., 2020).

4. CONCLUSION

This study confirmed the presence of SMV in soybean cultivated in Uzbekistan through RT-PCR, PCR, and sequence analysis of the coat protein (CP) gene. Phylogenetic analysis showed that the Uzbek isolate (TH-UZB1, GenBank accession no. OQ385206.1) clusters closely with Korean SMV isolates and shares high nucleotide identity with the Serbian isolate NDS_21. The biological characterization further demonstrated that the virus had a dilution end point of 10^{-4} and lost infectivity after heat treatment at 70°C. These findings provide the first molecular characterization of SMV in soybean from Uzbekistan and establish a baseline for future studies on the genetic diversity, epidemiology, and distribution of SMV populations in the country. The results also provide valuable information to support disease surveillance, resistance breeding, and the development of effective management strategies for sustainable soybean production.

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CONFLICT OF INTEREST
The authors declare no conflicts of interest.

AUTHOR CONTRIBUTION
Shuhrat Jumayorov: Conceptualization, Methodology, Writing - original draft. Tohir Xusanov: Investigation, Data collection. Zakhro Akhmedova: Formal analysis, Visualization. Zukhra Kadirova: Methodology, Validation. Abdirasul Vaxobov: Resources, Supervision. Xasan Sagdiyev: Software, Data curation. Nigora Nazarova: Writing - review and editing. Masudjon Sattarov: Supervision, writing-review and editing.

DATA AVAILABILITY
The nucleotide sequence of the coat protein gene of the Uzbekistan SMV isolate is available in GenBank under accession OQ385206.1. Other data generated or analyzed during this study are included in this published article.

DECLARATION OF GENERATIVE AI
Not applicable.

ETHICS
Not applicable.

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