

Molecular and biological characterization of squash leaf curl China virus infecting Phaseolus vulgaris in China

Jiao Du

Shuhong Li

Xiaonan Yang

Subing Hao

Jinting Li

Rongrui Tian

Songtao Zhang

Pengbai Li

lipengbai930409@163.com

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Abstract

Common bean (*Phaseolus vulgaris*) is one of the most economically vital vegetable crops in China. In June 2024, *Phaseolus vulgaris* samples displaying symptoms of leaf curling and crinkling were collected from an area adjacent to a pumpkin field in Zhengzhou, Henan Province, China. Full-length viral components were successfully isolated from the diseased *Phaseolus vulgaris* plants. The genome of the isolated virus was found to be 2,737 nucleotides (nt) in length, sharing the highest sequence similarity (99.3% identity) with that of the squash leaf curl China virus (SLCCNV). The DNA-B component consists of 2,717 nucleotides (nt) and shows the highest sequence similarity (98.5% identity) with the DNA-B segment of SLCCNV-SDZBZ. Pathogenicity assays demonstrated that inoculating *Phaseolus vulgaris* plants with both SLCCNV and SLCCNB led to the manifestation of typical leaf-curling and crinkling symptoms. The presence of the virus in the inoculated *Phaseolus vulgaris* plants was confirmed via polymerase chain reaction (PCR). To the best of our knowledge, this is the first report of SLCCNV and SLCCNB infecting *Phaseolus vulgaris* in China. These findings will contribute to the formulation of more effective management strategies against emerging viral threats.

Introduction

Geminiviruses are a group of single-stranded circular DNA viruses that have a detrimental impact on numerous crops, causing substantial economic losses (Navas-Castillo et al. 2011). Squash leaf curl China virus (SLCCNV), a member of the genus *Begomovirus* within the family *Geminiviridae*, is mainly transmitted by *Bemisia tabaci* (Hong et al. 1995). Its genome is composed of DNA-A and DNA-B components, each sized between 2.5 and 3.0 kb. DNA-A encodes seven proteins: AV1, AV2, AC1, AC2, AC3, AC4, and AC5, whereas DNA-B encodes two proteins: BV1 and BC1 (Wu et al. 2022).

SLCCNV was first identified in the field of pumpkin exhibiting leaf curl symptoms in Nanning, Guangxi Province in the 1990s (Hong et al. 1995). Subsequently, it has been reported in pumpkins across various countries, including Vietnam, India, the Philippines, Thailand, Pakistan, East Timor, and others (Revill et al. 2003; Singh et al. 2009; Maina et al. 2017; Venkataravanappa et al. 2021). In China, the virus has been documented in provinces such as Guangxi, Henan, Yunnan, and Hainan (Qiu et al. 2022). Previous research indicates that SLCCNV primarily infects cucurbit crops, such as pumpkin, gourd, winter melon, cucumber, melon, and cantaloupe, and induces typical symptoms including stunted growth, wilting leaves, and downward-curling leaf edges, resulting in significant economic losses in cucurbit agriculture (Wu et al. 2020). Recently, it has been reported that the host range of SLCCNV is gradually expanding. For example, in Indonesia, SLCCNV has been documented to naturally infect *Phaseolus vulgaris*; however, no such reports exist in China. Moreover, SLCCNV can also naturally infect other plants, such as tomato, posing potential threats to agricultural production (Qiu et al. 2022).

Common bean (*Phaseolus vulgaris*) is one of the most economically significant vegetable crops in China. It has been reported that begomoviruses can infect *Phaseolus vulgaris*, including tomato yellow leaf curl virus (TYLCV), cotton leaf crumple virus (CLCrV), tomato yellow leaf curl China virus (TYLCCNV),

tobacco curly shoot virus (TbCSV), and SLCCNV (Ji et al. 2012; Li et al. 2019). Among these, SLCCNV has not been reported to naturally infect *Phaseolus vulgaris* in China. In this study, we isolated and identified SLCCNV from *Phaseolus vulgaris* samples with curled and wrinkled leaves. Subsequently, we constructed an infectious clone to inoculate *Phaseolus vulgaris*, which resulted in the appearance of typical viral disease symptoms. This is the first report of SLCCNV infecting *Phaseolus vulgaris* in China.

Materials and methods

Samples collection

In 2024, two samples of *Phaseolus vulgaris* plants leaves displaying typical leaf curl and crinkling symptoms, as well as *Bemisia tabaci* on *Phaseolus vulgaris* plants, were collected in Henan Province of China.

Determination of full-length viral genomic sequences

Total DNA was extracted from the collected plant tissue samples using the CTAB method as previously described (Allen et al. 2006). A degenerate primer pair (PA: TAATATTACCKGWKGVCCSC; PB: TGGACYTTRCAWGGBCCTTCACA), which is conserved for all members of the genus *Begomovirus*, was employed to detect potential begomoviruses (Deng et al. 1994). The PCR products were separated by 1% agarose gel electrophoresis. The approximately 500 bp DNA fragment was purified and cloned into the pGEM-T Easy Vector (Promega, Madison, WI, USA) for sequencing. Based on the sequencing results, a pair of primers, Y-full-F/Y-full-R (Table S1), was designed to amplify the full-length DNA.

Total DNA was used as a template for rolling-circle amplification (RCA) with ϕ 29 DNA polymerase (TempliPhi kit, GE Healthcare). The RCA products were digested with *Cla*I. The approximately 3.0-kb digested products were purified and ligated into the pGEM-3Zf vector (Promega Corporation, Madison, WI, USA). Recombinant plasmid DNAs were transformed into *Escherichia coli* DH5 α , and selected clones were sequenced.

Phylogenetic analyses

The complete nucleotide sequences of SLCCNV DNA-A and DNA-B obtained through sequencing were subjected to BLAST analysis in NCBI. The sequences were processed using DNASTar and DNAMAN Version 4.0, and multiple sequence alignment was performed using the MUSCLE alignment method in DNASTar. The genomic organization of DNA-A and DNA-B was predicted using ORF Finder (<http://www.ncbi.nlm.nih.gov/gorf/gorf.html>). Phylogenetic trees were constructed using the maximum likelihood method in MEGA11 software with 1000 bootstrap replications (Tamura et al. 2011).

Infectious clone construction

To investigate the infectivity of SLCCNV/SLCCNB, two infectious clones of SLCCNV/SLCCNB (isolate HN1) were constructed using seamless cloning. First, the full-length genome of SLCCNV and SLCCNB were amplified using the primer pair A-InFu-F1/A-InFu-R1 and B-InFu-F1/B-InFu-R1 (Table S1), respectively, and these fragments were named 1.0A and 1.0B. Second, the primer pairs A-InFu-F2/A-InFu-R2 and B-InFu-F2/B-InFu-R2 (Table S1) were used to amplify the 0.9-mer fragment (0.9A and 0.9B) of SLCCNV and SLCCNB. Finally, the 1.0A and 0.9A fragments were inserted into the pBinPLUS vector via a seamless cloning method to generate the recombinant plasmids pBinPLUS-1.9A and pBinPLUS-1.9B. The ClonExpress MultiS One Step Cloning Kit (Vazyme, Nanjing, China) was used to perform the seamless cloning assays.

Agro-infiltration assays

The recombinant pBinPLUS-based expression vectors were transformed into *Agrobacterium tumefaciens* strain GV3101 pSoup. *A. tumefaciens* GV3101 pSoup was grown at 28°C for 2 days on Luria Bertani (LB) solid medium supplemented with rifampicin (20 µg/ml) and kanamycin (50 µg/ml). Subsequently, the *A. tumefaciens* was transferred to LB liquid medium containing the corresponding antibiotics and cultivated overnight in a 28°C shaker. *Agrobacterium* cells were collected by centrifugation and resuspended with inoculation buffer (10 mM MES, 200 µM acetosyringone, 10 mM MgCl₂) to OD₆₀₀ = 1.0. Then, the bacterial culture was infiltrated into the leaves of *Phaseolus vulgaris* plants using a aseptic syringe. Inoculations with the *Agrobacterium* strain carrying a pBinPLUS empty vector were used as a negative control. For the inoculation experiment, 10 biological replicates were included for each treatment, and three independent replicate experiments were conducted.

Results

Identification of begomovirus in *Phaseolus vulgaris*

In June 2024, *Phaseolus vulgaris* plants exhibiting leaf curl and crinkling symptoms were observed around pumpkin fields in Zhengzhou, Henan province, China (Fig. 1a). Concurrently, a large population of *Bemisia tabaci* was found on the undersides of the leaves (Fig. 1b). Samples from two diseased leaves (designated as HN1 and HN2) were collected, and tested by PCR. The results showed that the *Phaseolus vulgaris* samples were infected by begomovirus. Based on this sequence, a pair of primers, Y-full-F and Y-full-R, was utilized to amplify full-length viral genome sequences (Table S1). Analysis of the two full-length viral genome sequences (HN1 and HN2, GenBank accession numbers PQ373815 and PQ373816) revealed that both sequences contained 2737 nucleotides (nts). Comparative sequence analysis showed that the full-length sequences exhibited the highest sequence similarity (99.3%) with the SLCCNV isolate YN5946 (GenBank accession number MK626654). To confirm the above result, we performed a rolling-circle amplification (RCA) assay. Restriction enzyme digestion of the RCA products yielded a distinct 3.0-kbp fragment, and sequencing of this fragment was consistent with the full-length sequence obtained by PCR amplification (Figs. 1). Furthermore, we extracted total DNA from the preserved *Bemisia tabaci*

samples and performed PCR assays using SLCCNV-specific primers. The results indicated the presence of SLCCNV in *Bemisia tabaci* (Figs. 2).

To determine whether the two isolates contained DNA-B components or satellite molecules, degenerate DNA-B-specific primer pairs (CR01/CR02), betasatellite-specific primer pairs (beta01/beta02), and alphasatellite-specific primer pairs (UN101/UN102) were employed for PCR detection (Fondong et al. 2000; Briddon et al. 2002; Bull et al. 2003;). The results confirmed that both isolates contained DNA-B components without any other components present. The full-length nucleotide sequences of the HN1 and HN2 DNA-B components each comprised 2717 nts (PQ373817 and PQ373818) and shared 98.5% sequence identity with that of the SLCCNV-SDZBZ segment DNA-B (GenBank accession number OM258180).

Phylogenetic relationship between SLCCNV/SLCCNB and other geminiviruses

To investigate the phylogenetic relationships of the HN1 and HN2 DNA-A and DNA-B components with other begomoviruses, we constructed a phylogenetic tree using full-length viral genome sequences. The phylogenetic tree analysis indicated that the DNA-A components of HN1 and HN2 clustered into a small branch with SLCCNV and SLCV (Fig. 2a), indicating their close genetic relationship. In contrast, they exhibited a relatively distant relationship with SPLCV. Meanwhile, the DNA-B components of HN1 and HN2 grouped closely with other bipartite begomoviruses, with the highest relatedness to SLCCNB, while displaying a relatively distant genetic relationship with satellite molecules of some monopartite begomoviruses (Fig. 2b).

Pathogenicity test

To assess the pathogenicity of SLCCNV in *Phaseolus vulgaris*, infectious clones of SLCCNV and SLCCNB were constructed, and *Phaseolus vulgaris* plants were inoculated through agro-infiltration. Ten days post-inoculation (dpi), the plants inoculated with SLCCNV and SLCCNB displayed pronounced leaf curl and wrinkling symptoms compared to control plants (Fig. 3a). Subsequently, samples were collected for total DNA extraction and PCR analysis (Table S1), confirming the presence of both SLCCNV and SLCCNB (Fig. 3b, c). Meanwhile, statistical analysis of the infection efficiency of SLCCNV in inoculated *Phaseolus vulgaris* plants revealed an artificial inoculation success rate of 73.3% (22/30). In conclusion, SLCCNV and SLCCNB can successfully infect *Phaseolus vulgaris*, leading to typical viral symptoms.

Discussion

In this study, we successfully obtained two full-length viral genome sequences of SLCCNV from *Phaseolus vulgaris* samples, which showed 99.9% similarity, and provided comprehensive molecular characterization and information regarding the infectivity of SLCCNV in *Phaseolus vulgaris*. Our findings

demonstrated that SLCCNV can naturally infect *Phaseolus vulgaris* in the field, leading to severe diseases. This discovery holds great significance for the safe production of *Phaseolus vulgaris*. To the best of our knowledge, this is the first report of SLCCNV infecting *Phaseolus vulgaris* in China.

Over the past 50 years, geminiviruses have consistently remained among the most prominent pathogens affecting cultivated crops in most tropical and subtropical regions globally (Rojas et al. 2018). For example, cotton leaf curl disease (CLCuD), caused by cotton leaf curl Multan virus (CLCuMV), has had a severe impact on the cotton industries in Pakistan and India (Briddon et al. 2000; Sattar et al. 2013). Similarly, tomato yellow leaf curl disease (TYLCD), caused by TYLCV, has devastated tomato crops worldwide, resulting in hundreds of millions of dollars in annual economic losses (Lefeuvre et al. 2010; Prasad et al. 2020; Cao et al. 2024). In China, geminivirus-caused diseases are widespread and continue to spread (Rojas et al. 2018). Notably, SLCCNV, a significant member of the *Begomovirus* genus, has caused severe damage and economic losses to cucurbit crop production (Wu et al. 2020). In this study, the presence of SLCCNV was detected in *Phaseolus vulgaris* plants, indicating that both the host range and geographical distribution of SLCCNV are continuously expanding. This expansion poses increasingly severe threats and has a high potential for epidemic outbreaks.

The escalation of a disease pandemic is influenced by the population density of the vector, the viral load within the vector, the disease progression, and the growth stage of the plant (Lu et al. 2017). *Bemisia tabaci* is a crucial vector for the transmission of begomoviruses (Rogas et al. 2018). In recent years, with the rapid expansion of international food trade and the impacts of global warming, the population of *Bemisia tabaci* has increased significantly in many regions of China, leading to outbreaks of geminiviruses (Tang et al. 2008; Islam et al. 2018). In northern China, the widespread construction of greenhouses provides an extensive winter habitat for a large number of *Bemisia tabaci*. In this study, a considerable number of *Bemisia tabaci* were found on the leaves of *Phaseolus vulgaris*, and SLCCNV was also detected in *Bemisia tabaci*. This led us to hypothesize that SLCCNV may be transmitted from pumpkin plants to *Phaseolus vulgaris* via *Bemisia tabaci*. Therefore, effective management of *Bemisia tabaci* transmission is a critical strategy for preventing and controlling this viral disease.

Constructing infectious clones is a pivotal approach for studying viral pathogenicity. In this study, seamless cloning was used to successfully construct infectious clones of SLCCNV and its associated betasatellite (SLCCNB). Pathogenicity assays showed that inoculating of *Phaseolus vulgaris* plants with both SLCCNV and SLCCNB resulted in typical leaf curl and wrinkling symptoms, indicating that the virus may pose a significant threat to the secure production of *Phaseolus vulgaris*. With the migration and activity of *Bemisia tabaci*, the range of SLCCNV infection in *Phaseolus vulgaris* may gradually expand. Subsequently, disease surveillance for SLCCNV should be promptly carried out in *Phaseolus vulgaris* cultivation areas to clarify its occurrence status. For unaffected regions, quarantine measures should be strengthened to ensure the planting of virus-free seedlings, effectively controlling the spread and epidemic of SLCCNV. Additionally, efforts should be intensified to breed new *Phaseolus vulgaris* varieties resistant to SLCCNV, which would effectively prevent damage caused by SLCCNV in *Phaseolus vulgaris* plants.

Declarations

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Author contribution

All authors contributed to the study conception and design. Conceptualization: Jiao Du, Shuhong Li, Songtao Zhang, Pengbai Li; Design and methodology: Jiao Du, Songtao Zhang, Pengbai Li; Experiment execution and analysis: Jiao Du, Shuhong Li, Xiaonan Yang, Subing Hao, Jinting Li, Rongrui Tian; The first original draft preparation: Jiao Du; Writing, rewriting and editing: Jiao Du, Songtao Zhang, Pengbai Li; supervision: Songtao Zhang, Pengbai Li; All the authors gave final approval of the published version.

Compliance with ethical standards

I have read and have abided by the statement of ethical standards for manuscripts submitted to Journal of Plant Diseases and Protection.

Conflict of interest

All authors declare they have no conflict of interest.

Ethical approval

This article does not contain any studies with human participants or animal performed by any of the authors.

Data availability statement

All data generated or analysed during this study are included in this published article. Further inquiries for additional information can be directed to the corresponding authors.

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Figures

a



b



Figure 1

a Symptomatic *Phaseolus vulgaris* plant exhibiting leaf curl and crinkling symptoms; **b** A large population of *Bemisia tabaci* exist on the undersides of the leaves.

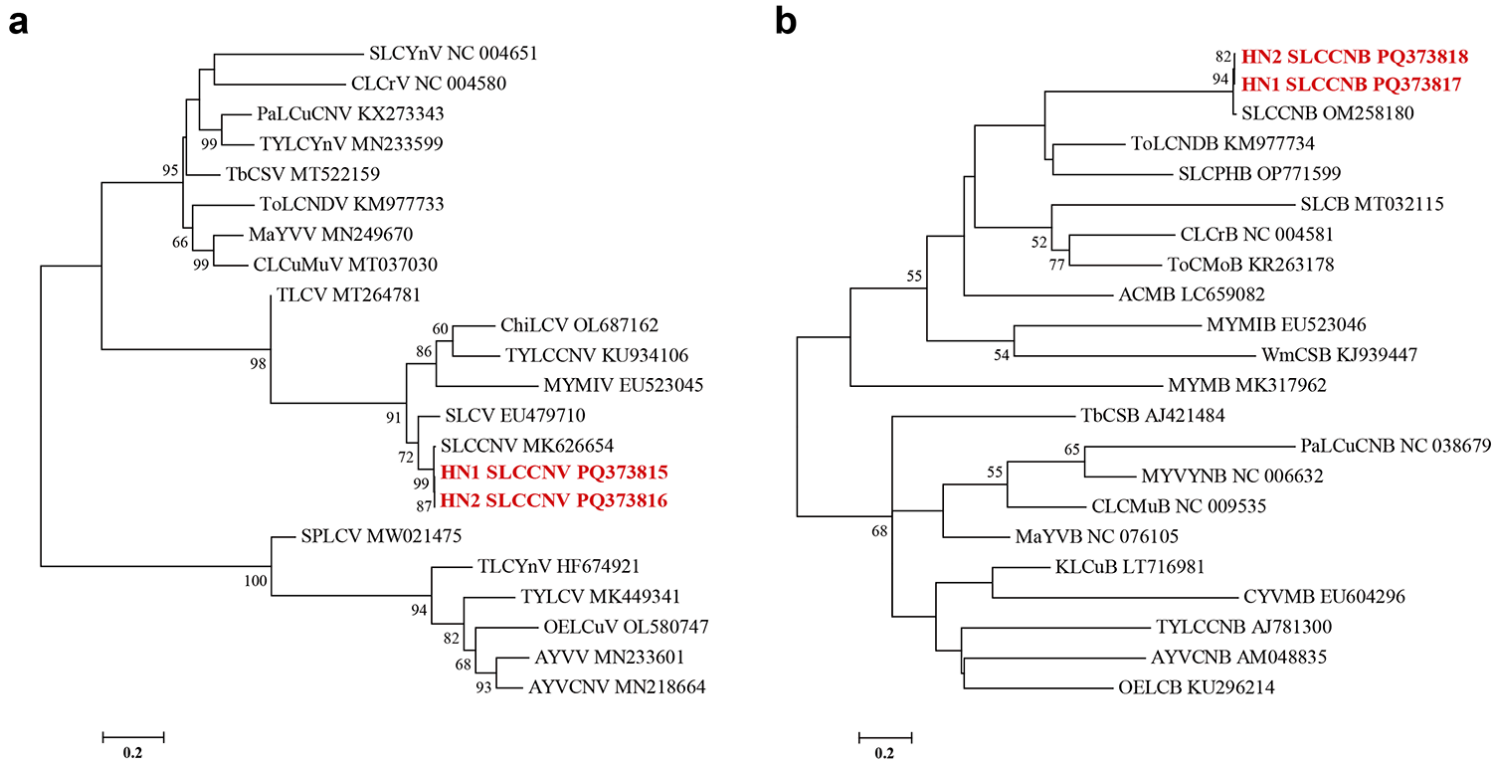


Figure 2

a Phylogenetic tree illustrating the relationships between the SLCCNV sequences and other previously reported begomovirus sequences. **b** Phylogenetic tree illustrating the relationships between the SLCCNB sequences and other previously reported begomovirus sequences. The tree was produced by the maximum-likelihood method with 1000 bootstrap replications, using MEGA 11 software. Squash leaf curl Yunnan virus (SLCYnV), cotton leaf crumple virus (CLCrV), papaya leaf curl China virus (PaLCuCNV), tomato yellow leaf curl Yunnan virus (TYLCYnV), tobacco curly shoot virus (TbCSV), tomato leaf curl New Delhi virus (ToLCNDV), malvastrum yellow vein virus (MaYVV), cotton leaf curl Multan virus (CLCuMuV), tomato leaf curl virus (TLCV), chilli leaf curl virus (ChiLCV), tomato yellow leaf curl China virus (TYLCCNV), mungbean yellow mosaic India virus (MYMIV), squash leaf curl virus (SLCV), sweet potato leaf curl virus (SPLCV), tomato leaf curl Yunnan virus (TLCYnV), tomato yellow leaf curl virus (TYLCV), okra enation leaf curl virus (OELCuV), ageratum yellow vein virus (AYVV), ageratum yellow vein China virus (AYVCNV).

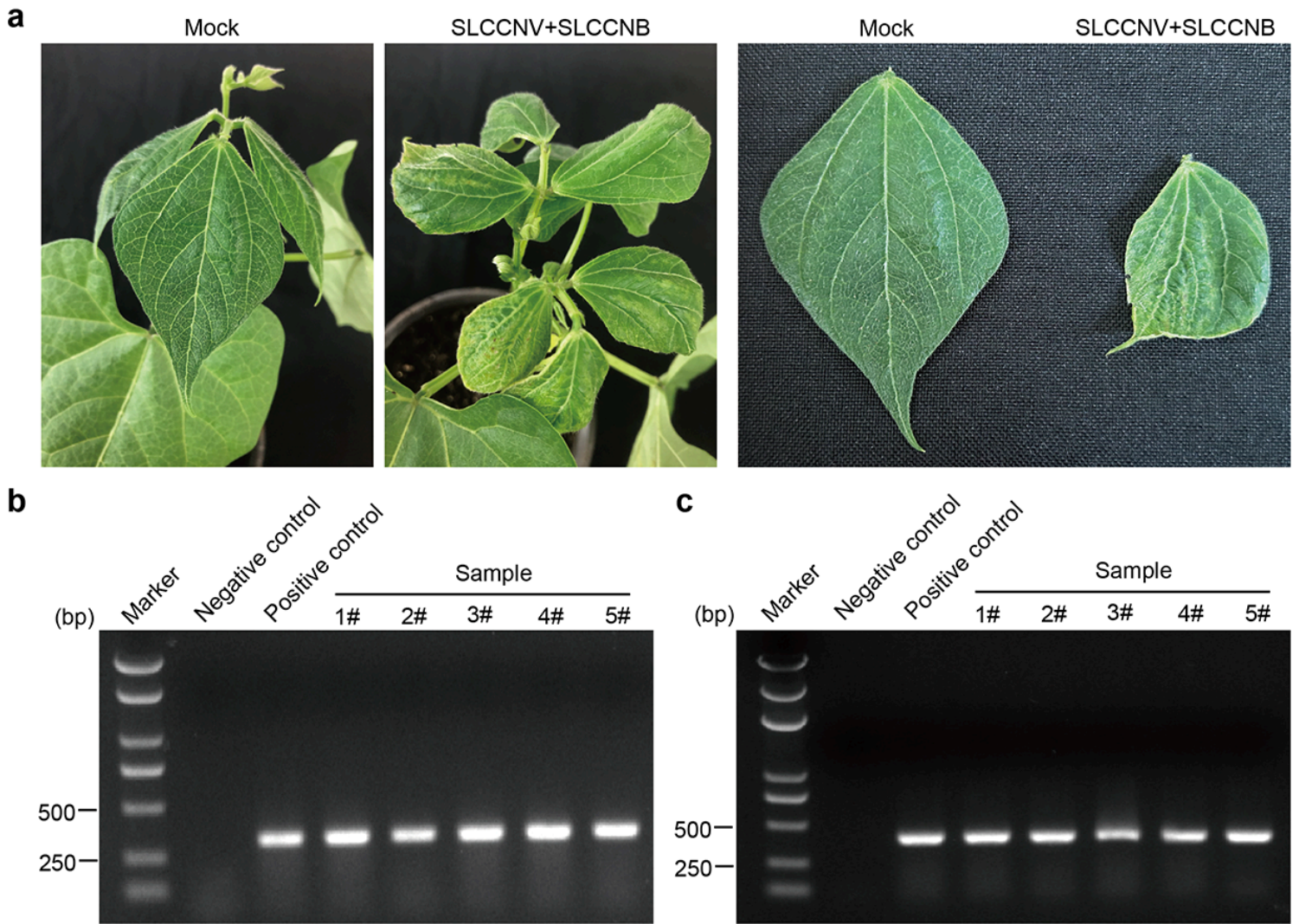


Figure 3

a Symptoms induced by SLCCNV and SLCCNB infection in *Phaseolus vulgaris* plants. The *Phaseolus vulgaris* plants infected with SLCCNV and SLCCNB showed leaf curl and wrinkling symptoms. The pictures were taken at 10 days post-inoculation (dpi); **b** Detection of DNA-A component of SLCCNV in inoculated *Phaseolus vulgaris* plants; **c** Detection of DNA-B component of SLCCNV in inoculated *Phaseolus vulgaris* plants.

Supplementary Files

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