Journal of Tropical Biodiversity and Biotechnology
Volume 10, Issue 02 (2025): jtbb15670
DOI: 10.22146/jtbb.15670

Short Communication

Evaluation of Krusty/Homer and SPG1/SPG2 Primer Pairs in Identification of Six Begomoviruses Commonly Found in Indonesia

Nabilla Kurnialaili Defitra[1], Hayu Alifia Zahra[1], Antama Surwadinata[1], Rachmad Saputra[1,2], Aprilia Sufi Subiastuti[3], Mayadah A. Haj Ali[4,5], Adyatma Irawan Santosa[1]*

1)Department of Plant Protection, Faculty of Agriculture, Universitas Gadjah Mada, Sleman 55281, Indonesia
2)Plant Protection Study Program, Agrotechnology Department, Agriculture Faculty, Universitas Riau, Kota Pekanbaru 28293, Indonesia
3)Laboratory of Microbiology, Faculty of Biology, Universitas Gadjah Mada, Sleman 55281, Indonesia
4)Department of Plant Pathology, International Centre for Agricultural Research in the Dry Areas (ICARDA), Cairo 11728, Egypt
5)Department of Microbiology and Immunology, National Commission for Biotechnology (NCBT), Damascus, Syria
* Corresponding author, email: adyatma.i.s@ugm.ac.id

Keywords:
Molecular variation
PCR
Phylogenetic tree
Plant DNA virus
Plant viral disease
Submitted:
10 August 2024
Accepted:
11 December 2024
Published:
28 April 2025
Editors:
Miftahul Ilmi
Liya Audinah

ABSTRACT

Fourteen symptomatic crops and weeds from Magelang, Klaten, Sleman, and Bantul Regencies were tested against begomoviruses using Krusty/Homer and SPG1/SPG2 primer pairs. The acquired nucleotide sequences were involved in phylogenetic analysis which clustered isolates into six species. Furthermore, three recombinant isolates were also identified. Protocol for molecular characterization of prevalent begomoviruses using both primer pairs was initiated in this report. Molecular data of the obtained 14 isolates added important information on the genetic diversity of Indonesian isolates.

How to cite:
Defitra, N.K. et al., 2025. Evaluation of Krusty/Homer and SPG1/SPG2 Primer Pairs in Identification of Six Begomoviruses Commonly Found in Indonesia. *Journal of Tropical Biodiversity and Biotechnology*, 10(2), jtbb15670. doi: 10.22146/jtbb.15670

Begomovirus, a genus within the family Geminiviridae, has single-stranded DNA genomes encapsidated in twinned particles approx. 22 × 38 nm in size. Its members are persistently transmitted by whitefly (*Bemisia tabaci*), and pose significant threats to agricultural productivity, especially in the tropical and subtropical regions (Fiallo-Olivé & Navas-Castillo 2023). Similar situation in Indonesia, begomoviruses are still real concerns for the cultivation of economically valuable *Solanaceae*, *Cucurbitaceae*, and *Fabaceae* crops (Santosa & Somowiyarjo 2023; Wahyono et al. 2023). Thus, accurate detection and thorough molecular characterization of these viruses are crucial for disease management in the country (Subiastuti et al. 2019).

Universal primer pairs such as Krusty/Homer (KH) (Revill et al. 2003) and SPG1/SPG2 (SPG) (Li et al. 2004) have been widely employed for detection of begomoviruses. These primers enable the amplification of a broad spectrum of begomovirus genomes, facilitating the identification up to species level in a single assay. Moreover, these primer pairs have been effectively proven in different crops and geographic regions. KH primer pair is developed to target ± 580-base pair (bp) of partial *AV1* gene (coat protein/CP gene) of the begomovirus genome which is a highly conserved region (Figure 1), allowing for detection of diverse species (Revill et al. 2003). Meanwhile, SPG primer pair is designed to amplify ± 912 bp partial fragment of *TrAP* and *Rep* genes of begomoviruses (Figure 1). Therefore, not only having a high degree of specificity and sensitivity but also SPG covers up to one third of DNA-A segment, making it a valuable tool for studying variations in the viruses (Li et al. 2004).

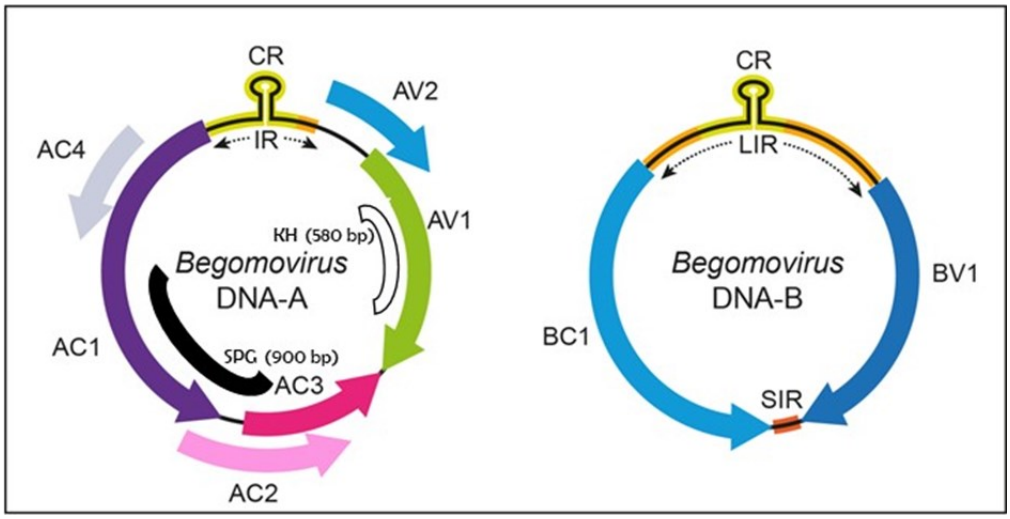

Figure 1. Schematic provided by ICTV (https://ictv.global) shows bipartite genome of begomovirus with bidirectional genome organization of AV1, AV2, AC1, AC2, AC3, and AC4 genes in DNA-A, and BV1 and BC1 genes in DNA-B, respectively. Approximate positions of regions within DNA-A segment of begomovirus genome amplified by Krusty/Homer primer pair (white area) and SPG1/SPG2 primer pair (black area).

In Indonesia, applications of KH and SPG primers has led to the identification of several major begomovirus species. For instance, tomato yellow leaf curl Kanchanaburi virus (TYLCKaV), squash leaf curl China virus (SLCCNV), pepper yellow leaf curl Indonesia virus (PepYLCIV), and papaya leaf curl virus (PaLCV) have been detected respectively in eggplant (*Solanum melongena*), squash (*Cucurbita pepo*), chili pepper (*Capsicum annuum*), and papaya (*Carica papaya*) cultivated in regions such as Java, Lampung, Bali, and Bengkulu using SPG primer (Kintasari et al. 2013; Wiratama et al. 2015; Sutrawati et al. 2021; Selangga & Listihani 2021; Akin et al. 2023). Additionally, mung bean yellow mosaic India virus (MYMIV), PepYLCIV, TYLCKaV, and

SLCCNV were reported in *Solanaceae*: chili pepper and eggplant, *Cucurbitaceae*: angled luffa (*Luffa acutangular*) and squash, and *Fabaceae*: mung bean (*Vigna radiata*) crops in Yogyakarta, Southeast Sulawesi, Lampung, and Central Java using KH primer (Wilisiani et al. 2014; Subiastuti et al. 2019; Giovanni et al. 2020; Mulyadi et al. 2021; Taufik et al. 2023; Akin et al. 2023; Santosa et al. 2024). Therefore, these viruses were also shown to be widespread and infecting different plant groups in Indonesia (Wiratama et al. 2015; Listihani et al. 2019; Sutrawati et al. 2021; Taufik et al. 2023).

By enabling rapid and accurate identifications of multiple begomovirus species, KH and SPG primers play crucial roles in the management of virus-induced diseases in crops. Despite covering different regions, these primers have only been used separately in molecular detection protocols and have never been involved in the molecular characterization of the same isolate in Indonesia. This study aims to evaluate both universal primer pairs in the molecular characterization of six begomovirus species widespread in Indonesia. It also seeks to expand our understanding of the genetic diversity of isolates infecting important horticultural commodities and weeds at observed locations.

Leaves of horticultural crops and weeds with conspicuous begomovirus symptoms were collected during field surveys in Magelang, Klaten, Sleman, and Bantul Regencies in January – June 2024. Samples were purposively taken based on viral symptom appearances then brought to Phytopathology Laboratory, Universitas Gadjah Mada to be kept at -4 °C until further analysis shortly.

Total DNA from each collected samples were extracted using Genomic DNA Mini Kit for Plant following standard steps suggested by the manufacturer (Geneaid Biotech Ltd., Taiwan). PCRs for each sample were subsequently done twice each using either of two universal primer pairs for begomoviruses detection: Krusty (F 5`-CCNMRDGGHTGTGARGGNCC-3`)/ Homer (R 5`-SVDGCRTGVGTRCANGCCAT-3`) targeting ± 580 bp of partial *AV1* gene (Revill et al. 2003) and SPG1 (F 5`-CCCCKGTGCGWRAATCCAT-3`)/SPG2 (R 5`-ATCCVAAYWTYCAGGGAGCT-3`) amplifying ± 900 bp partial *AC1* and *AC2* genes (Li et al. 2004). Each PCR reaction was prepared in a volume of 40 µl: 2 µl (10 pmol μl^{-1}) each of reverse primer and forward primer, 20 µl of MyTaq HS Red Mix (Bioline, Germany), 4 µl of DNA template, and 12 µl of PCR-grade water. The PCR cycle is organized as follows pre-denaturation step at 96 °C for 3 minutes, followed by 35 cycles of denaturation at 96 °C for one minute, annealing 55 °C for KH and 59 °C for SPG, each lasting 1 minute, elongation at 72 °C for 1 minute, and lastly final elongation at 72 °C for 10 minutes.

PCR products were loaded into wells of agarose gel stained with Florosafe DNA Staining (1st BASE, Malaysia), and then electrophoresis for the gel was run for 50 minutes at 50 V. The appearance and size of PCR bands were examined under a UV transilluminator (Optima Inc., Japan). Successful amplified PCR products were submitted to LPPT UGM for Sanger sequencing bidirectionally. Nucleotide sequences of partial *AV1*, and partial *AC1* and *AC2* genes of each isolate were expected to be established by this strategy. Determination of species of isolates was performed using nucleotide BLAST online software (https://blast.ncbi.nlm.nih.gov) which paired the new nucleotide sequences with those available in NCBI GenBank database. Nucleotide sequences of the novel isolates were then registered in GenBank to obtain unique accession numbers.

Begomovirus isolates with complete genome sequences registered in GenBank were aligned with and then trimmed according to the lengths of sequences of the newly obtained isolates using ClustalW algorithm in

MEGA11 software (Tamura et al. 2021). Two phylogenetic trees, for partial *AV1* gene and partial *AC1* and *AC2* genes, were constructed with Maximum Likelihood (ML) statistical method and Tamura-Nei (Tamura & Nei 1993) parameter model implemented in MEGA11. Statistical significancy of each branch was tested with 1000 bootstrap replicates.

Possible recombination event on the genome of isolates positioned in different species groups of the constructed phylogenetic trees was scanned using Recombination Detection Program (RDP v5.30) (Martin et al. 2021). Only event detected by at least five of algorithms (Bootscan, MaxChi, Chimaera, 3Seq, Siscan, GENECONV, and RDP) suited in the software was considered convincing with significance of Bonferroni-corrected p value of < 0.05 (Martin et al. 2021).

In total, 14 samples: 4 chili peppers (*Capsicum annuum*), 1 tomato (*Solanum lycopersicum*), 1 eggplant (*Solanum melongena*), 3 squash (*Cucurbita pepo*), 2 melons (*Cucumis melo*), 2 yardlong bean (*Vigna unguiculata* ssp. *sesquipedalis*), and 1 billy goat weed (*Ageratum conyzoides*) were collected during field surveys then tested for begomovirus infection.

Results of PCR and the subsequent electrophoresis indicated begomovirus infection in all 14 tested samples by appearance of bands with specific sizes for KH primers and for SPG primers, respectively. BLAST analysis on the obtained sequences identified six begomoviruses: ageratum yellow vein China virus (AYVCNV), tomato yellow leaf curl Kanchanaburi virus (TYLCKaV), pepper yellow leaf curl Indonesia virus (PepYLCIV), squash leaf curl China virus (SLCCNV), mung bean yellow mosaic India virus (MYMIV), tomato leaf curl New Delhi virus (ToLCNDV) among the 14 isolates. GenBank accession nos. PP874885-94 and PQ112501-4 for partial *AV1* gene and nos. PP874895-904 and PQ112505-8 for partial *AC1* and *AC2* genes were assigned to the obtained sequences (Table 1). Symptoms on the begomovirus infected samples including chlorosis, mosaic, blisters, and dwarfing (Figure 2).

The laboratory work presented here identified a diverse species of *Begomovirus* infecting 13 commercial crops and 1 weed in four regencies in Java Island of Indonesia. All sampled plants exhibited clear and severe symptoms. ToLCNDV was previously detected in cucumber (*Cucumis sativus*) grown in Klaten (Listihani et al. 2019). Nidianti et al. (2023) recently found SLCCNV infection on a melon cultivar screened for breeding program in Sleman. Another recent report recorded PepYLCIV and SLCCNV in Magelang Regency, infecting chili pepper and squash, respectively (Santosa et al. 2024). Therefore, begomoviruses were shown to be still major problem hampering cultivation of different horticultural commodities and inciting economical losses in the surveyed areas.

KH and SPG primers were demonstrated to be conveniently used in PCR for molecular identification of six species of *Begomovirus*. As results, nucleotide sequences of two different genome regions (*AV1*, and *AC1* and *AC2*) of 14 isolates of the six begomoviruses were obtained using Sanger method in this study, and then the sequences were registered in NCBI GenBank.

Phylogenetic analysis of the obtained sequences formed two separate trees based on the genomic regions. Both trees clustered isolates into different phylogroups according to their respective species. The newly obtained isolates generally have a closer genetic relationship with previously reported Indonesian isolates, as shown by their share of common basal nodes, than isolates from other country. Two melon isolates from Bantul regency (MlBTL and MlBTL2) were in SLCCNV group in AV1 tree but positioned in ToLCNDV group in AC1-AC2 tree, which indicated recombination in their genomes and thus the necessity to further analysis using RDP software (Figure 3).

Table 1. Begomovirus isolates identified in this report

No.	Isolate name	Species[α]	Host	Origin	Genbank accession no.	
					Partial AV1 gene	Partial AC1 and AC2 genes
1.	ACSMN	AYVCNV	*Ageratum conyzoides*	Sleman	PP874885	PP874895
2.	TrMGG	TYLCKaV	eggplant	Magelang	PP874886	PP874896
3.	ToKLN-Kr	TYLCKaV	tomato	Klaten	PP874887	PP874897
4.	CbKLN-Kr	PepYLCIV	chili pepper	Klaten	PP874888	PP874898
5.	CbKLN-K	PepYLCIV	chili pepper	Klaten	PP874889	PP874899
6.	CbMGG	PepYLCIV	chili pepper	Magelang	PP874890	PP874900
7.	CbSMN	PepYLCIV	chili pepper	Sleman	PP874891	PP874901
8.	LbSMN	SLCCNV	squash	Sleman	PP874892	PP874902
9.	KPMGG	MYMIV	yardlong bean	Magelang	PP874893	PP874903
10.	KPSMN	MYMIV	yardlong bean	Sleman	PP874894	PP874904
11.	LbSMN2	SLCCNV-ToLCNDV[β]	squash	Sleman	PQ112501	PQ112505
12.	MlBTL	SLCCNV-ToLCNDV[β]	melon	Bantul	PQ112502	PQ112506
13.	MlBTL2	SLCCNV-ToLCNDV[β]	melon	Bantul	PQ112503	PQ112507
14.	LbSMN3	ToLCNDV	squash	Sleman	PQ112504	PQ112508

[α]ageratum yellow vein China virus = AYVCNV; tomato yellow leaf curl Kanchanaburi virus = TYLCKaV; pepper yellow leaf curl Indonesia virus = PepYLCIV; squash leaf curl China virus = SLCCNV; mungbean yellow mosaic India virus = MYMIV; tomato leaf curl New Delhi virus = ToLCNDV. [β]Recombinant isolates.

Recombination in the *AC1* and *AC2* regions of genomes of MlBTL and MlBTL2 was detected by RDP, Bootscan, MaxChi, Chimera, and 3Seq algorithms in RDP thus can be deduced as significant. WMK, a SLCCNV isolate from Indonesia, was revealed as the major parent of the two isolates while 17MY167A, a ToLCNDV isolate from Malaysia, was the minor parent. The RDP analysis also found a strong recombination signal in the genome of LbSMN2 with support from RDP, GENECONV, MaxChi, Chimaera, SiScan, and 3Seq algorithms. A SLCCNV isolate from Timor-Leste (T4D) was suggested to be the major parent while its minor parent was LbSMN3, a ToLCNDV isolate from Indonesia.

MBTL and MBTL2 isolates were included in SLCCNV cluster in KH tree while positioned in ToLCNDV group in SPG tree, strongly indicating recombination. MBTL and MBTL2 isolates which showed almost identical genetic sequences, at least in the observed regions, originated from two melon plants separated only around 25 m each other in the same greenhouse in Bantul Regency. These two were the only plants showing clear viral symptoms among >300 individuals in the greenhouse. RDP analysis confirmed MBTL and MBTL2 were SLCCNV recombinant isolates which received donor from ToLCNDV. Scan using RDP further detected a recombination signal in the genome of LbSMN2, which was also a SLCCNV isolate recipient of genetic donor from ToLCNDV. This recombination was unlikely observable if only one of primer pairs applied in the molecular diagnostic. Both SLCCNV and ToLCNDV are prone for recombination, and interspecies genetic exchange between them have been reported to occur naturally (Venkataravanappa et al. 2018). Another study demonstrated a case of intraviral recombination in the genome of an Indonesian ToLCNDV isolate

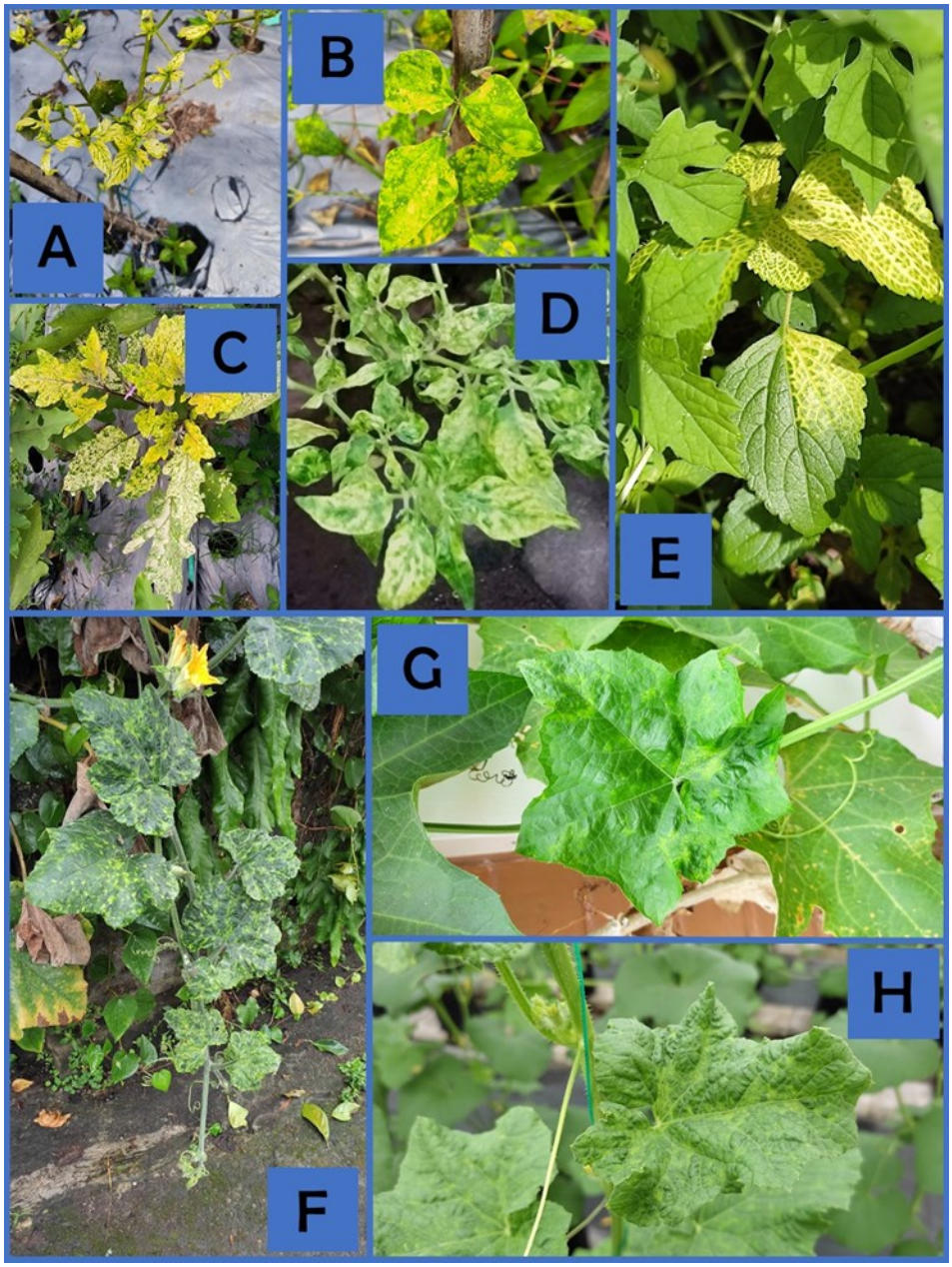

Figure 2. Variation of disease symptoms on horticultural crops caused by different begomoviruses reported in this study. A. Chlorosis and stunting on chili pepper infected by PepYLCIV isolate CbMGG in Magelang; B. Cholorosis on yardlong bean infected by MYMIV isolate KPMGG in Magelang; C. Chlorosis on eggplant infected by TYLCKaV isolate TrMGG in Magelang; D. Chlorosis on chili pepper infected by PepYLCIV isolate CbSMN in Sleman; E. Vein chlorosis on *Ageratum conyzoides* infected by AYVCNV isolate ACSMN in Sleman; F. Severe mosaic and blisters on squash infected by recombinant SLCCNV-ToLCNDV isolate LbSMN2 in Sleman; G. Severe mosaic on squash infected by ToLCNDV isolate LbSMN3 in Sleman; H. Mosaic on melon infected by recombinant SLCCNV-ToLCNDV isolate MlBTL2 in Bantul.

(Wilisiani et al. 2019). In begomoviruses, recombination may act as a mechanism that ensures the evolution path is stay adaptive to new hosts or changing environmental constraints (Vo et al. 2022).

Protocol for detection and molecular characterisation of begomoviruses using KH and SPG has been established in this report but both primer pairs need to be tested against other species to complement the efficacy data of these primers. Nucleotide sequences covered by both primers provided important genomic data of isolates, including recombination events. Therefore, future studies on identification of begomoviruses are recommended to use both primer pairs to reduce false negative in case a distinct recombinant breakpoint could not be detected by one of the primers. Additional nucleotide sequences of 14 begomovirus isolates improved our understanding of the ge-

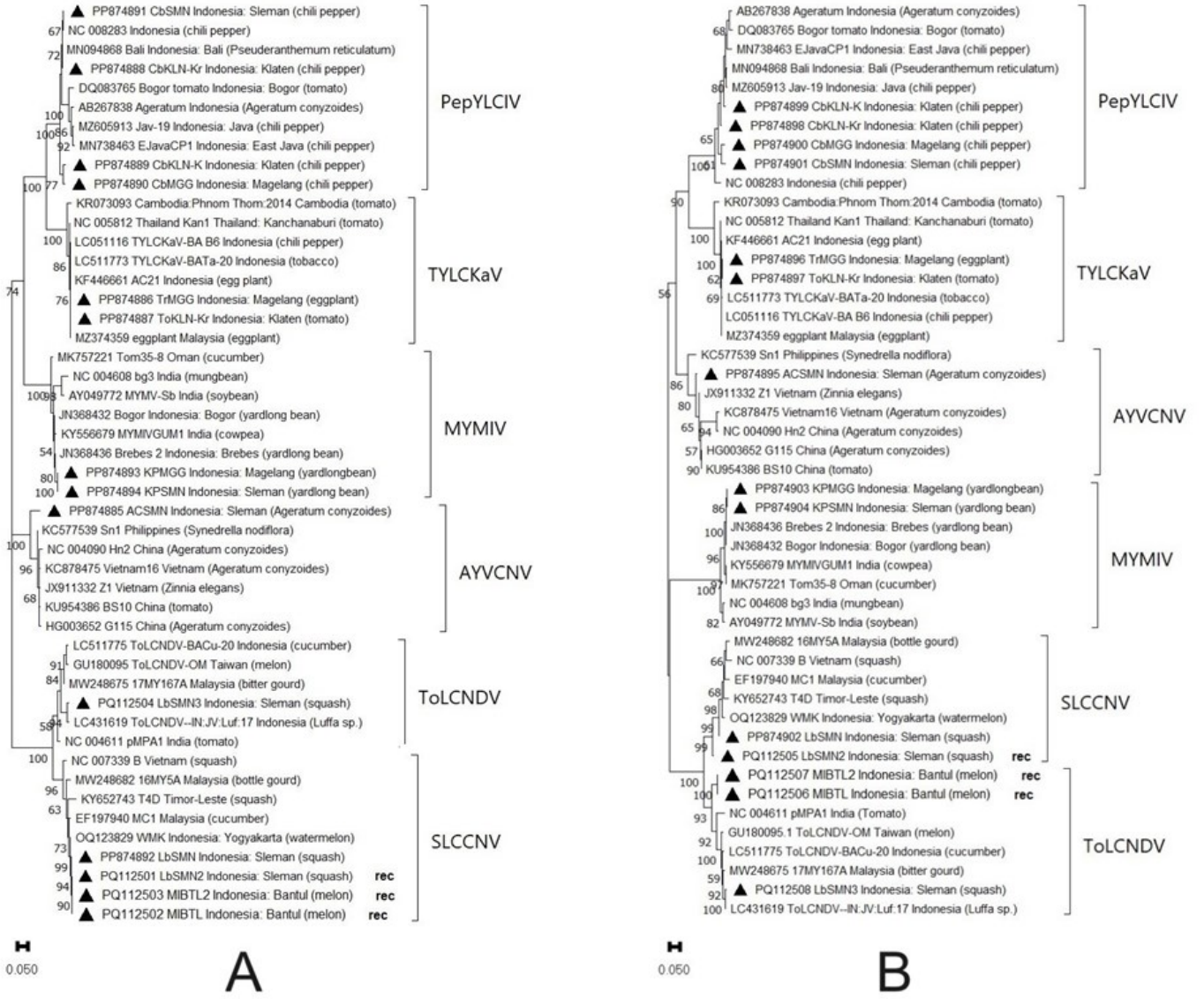

Figure 3. Phylogenetic trees based on nucleotide sequences of (A) ± 552 bp partial *AV1* gene targeted by Krusty/Homer primers and (B) ± 893 bp partial *AC1* and *AC2* genes covered by SPG1/SPG2 primers of isolates of six begomovirus species. The trees were generated in MEGA11 software by the Maximum-Likelihood method based on Tamura-Nei-parameter's model (1000 bootstrap replicates, only >50 % values were shown). Isolates reported here were marked with black triangles. SLCCNV and ToLCNDV recombinant isolates were marked with 'rec'. Ageratum yellow vein China virus = AYVCNV; tomato yellow leaf curl Kanchanaburi virus = TYLCKaV; pepper yellow leaf curl Indonesia virus = PepYLCIV; squash leaf curl China virus = SLCCNV; mungbean yellow mosaic India virus = MYMIV; tomato leaf curl New Delhi virus = ToLCNDV

nomic variance of Indonesian isolates. Further surveys are needed to study our local recombinant isolates that potentially cause outbreaks in the future, as have been observed in other countries (Moriones et al. 2017).

AUTHOR CONTRIBUTION

N.K.D. and H.A.Z. collected samples, conducted field observation, and performed laboratory research. A.S. performed laboratory research and wrote the draft manuscript. R.S. collected samples and conducted field observation. A.S.S. and M.A.H.A. analysed the data and revised the manuscript. A.I.S. designed and supervised the research, analysed the data, and wrote the draft manuscript.

ACKNOWLEDGMENT

This research received no external funding.

CONFLICT OF INTEREST

Authors have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

REFERENCES

Akin, H.M. et al., 2023. Biological and molecular characteristics of begomovirus mild strains and their elucidation for cross protection against eggplant begomovirus (*Solanum melongena* L.). *Pakistan Journal of Phytopathology*, 35(2), pp.215–222. doi: 10.33866/phytopathol.035.02.0931

Fiallo-Olivé, E. & Navas-Castillo, J., 2023. Begomoviruses: what is the secret (s) of their success? *Trends in Plant Science*, 28(6), pp.715–727. doi: 10.1016/j.tplants.2023.01.012

Giovanni, A.C. et al., 2020. Molecular identification of begomovirus infecting angled luffa. *Jurnal Perlindungan Tanaman Indonesia*, 24(2), pp.147–153. doi: 10.22146/jpti.31073

Kintasari, T. et al., 2013. Tomato yellow leaf curl Kanchanaburi virus penyebab penyakit mosaik kuning pada tanaman terung di Jawa (in Bahasa Indonesia). *Jurnal Fitopatologi Indonesia*, 9(4), pp.127–131. doi: 10.14692/jfi.9.4.127

Li, R., Salih S. & Hurtt, S., 2004. Detection of Geminiviruses in sweetpotato by polymerase chain reaction. *Plant Disease*, 88(12), pp.1347–1351. doi: 10.1094/PDIS.2004.88.12.1347

Listihani, L. et al., 2019. Molecular characterization of begomovirus on cucumber in Java. *Jurnal Perlindungan Tanaman Indonesia*, 23(2), pp.197–204. doi: 10.22146/jpti.41402

Martin, D.P. et al., 2021. RDP5: a computer program for analyzing recombination in, and removing signals of recombination from, nucleotide sequence datasets. *Virus Evolution*, 7(1), veaa087. doi: 10.1093/ve/veaa087

Moriones, E., Praveen, S. & Chakraborty, S., 2017. Tomato leaf curl New Delhi virus: An emerging virus complex threatening vegetable and fiber crops. *Viruses*, 9(10), 264. doi: 10.3390/v9100264

Mulyadi, D. et al., 2021. Distribution, host range and detection of seed-borne yellow mosaic disease on yardlong beans (*Vigna unguiculata* subsp. *sesquipedalis* L.) in the special region of Yogyakarta, Indonesia. *Biodiversitas*, 22(9), pp.3949–3957. doi: 10.13057/biodiv/d220942

Nidianti, E. et al., 2023. Biological response and molecular identification of the begomovirus infection in the new Indonesian melon genotype Kinaya. *Pakistan Journal of Phytopathology*, 35(2), pp.223–234. doi: 10.33866/phytopathol.035.02.0939

Revill, P.A. et al., 2003. The complete nucleotide sequence of two distinct geminiviruses infecting cucurbits in Vietnam. *Archives of Virology*, 148 (8), pp.1523–1541. doi: 10.1007/s00705-003-0109-6

Santosa, A.I. & Somowiyarjo, S., 2023. Ageratum yellow vein alphasatellite and tomato leaf curl Java betasatellite association with begomoviruses infecting crops and weeds in Indonesia. *Plant Protection Science*, 59(4), pp.317–324. doi: 10.17221/16/2023-PPS

Santosa, A.I. et al., 2024. Updates on hosts and distribution of pepper yellow leaf curl Indonesia virus and squash leaf curl China virus in Central Java Province, Indonesia. *Jurnal Ilmiah Pertanian*, 21(1), pp.11–20. doi: 10.31849/jip.v21i1.18856

Selangga, D.G.W. & Listihani., 2021. Molecular identification of pepper yellow leaf curl Indonesia virus on chili pepper in Nusa Penida Island. *Journal of Tropical Plant Pests and Diseases*, 21(2), pp.98–102. doi: 10.23960/jhptt.22197-102

Subiastuti, A.S., Hartono, S. & Daryono, B.S., 2019. Detection and identification of begomovirus infecting *Cucurbitaceae* and *Solanaceae* in Yogyakarta, Indonesia. *Biodiversitas*, 20(3), pp.738–744. doi: 10.13057/biodiv/d200318

Sutrawati, M. et al., 2021. First report of begomovirus infection on papaya in Bengkulu, Indonesia. *Journal of Tropical Plant Pests and Diseases*, 21(1), pp.49–55. doi: 10.23960/jhptt.12149-55

Tamura, K., Stecher, G. & Kumar, S., 2021. MEGA11: molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution*, 38(7), pp.3022–3027. doi: 10.1093/molbev/msab120

Tamura, K. & Nei, M., 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution*, 10(3), pp.512–526. doi: 10.1093/oxfordjournals.molbev.a040023

Taufik, M. et al., 2023. Sebaran penyakit daun keriting kuning pada pertanaman cabai di Sulawesi Tenggara dan indentifikasi penyebabnya (in Bahasa Indonesia). *Jurnal Fitopatologi Indonesia*, 19(3), pp.89–98. doi: 10.14692/jfi.19.3.89-98

Venkataravanappa, V. et al., 2018. Recombinant tomato leaf curl New Delhi virus is associated with yellow vein mosaic disease of okra in India. *Physiological and Molecular Plant Pathology*, 104, pp.108–118. doi: 10.1016/j.pmpp.2018.10.004

Vo, T.T.B. et al., 2022. ToLCNDV-ES infection in tomato is enhanced by TYLCV: Evidence from field survey and agroinoculation. *Frontiers in Microbiology*, 13, 954460. doi: 10.3389/fmicb.2022.954460

Wahyono, A. et al., 2023. Current status and complexity of three begomovirus species in pepper plants in lowlands and highlands in Java Island, Indonesia. *Viruses*, 15(6), 1278. doi: 10.3390/v15061278

Wilisiani F. et al., 2019. Complete genome sequence of tomato leaf curl New Delhi virus from luffa in Indonesia. *Microbiology Resource Announcements*, 8(15), e01605-18. doi: 10.1128/mra.01605-18

Wilisiani, F., Somowiyarjo, S. & Hartono, S., 2014. Identifikasi molekuler virus penyebab penyakit daun keriting isolat Bantul pada melon (in Bahasa Indonesia). *Jurnal Perlindungan Tanaman Indonesia*, 18(1), pp.47–54. doi: 10.22146/jpti.15602

Wiratama, I.D.M.P. et al., 2015. Laporan pertama infeksi begomovirus pada tanaman mentimun di Bali (in Bahasa Indonesia). *Jurnal Fitopatologi Indonesia*, 11(5), pp.175–178. doi: 10.14692/jfi.11.5.175