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Original article

Detection of Ageratum yellow vein China virus on weeds *Acalypha indica* L. and *Euphorbia heterophylla* L. in Indonesia

Endonezya'da *Acalypha indica* L. ve *Euphorbia heterophylla* L. yabancı otlarında Ageratum sarı damarlı Çin virüsünün belirlenmesi

Antama SURWADINATA[a], Ucik NUGROHO[a], Dea Putri NOVITASARI[a], Nadila VINATA[a], Filiz RANDA-ZELYÜT[b], Adyatma Irawan SANTOSA[a*]

https://orcid.org/0009-0008-3117-3314, https://orcid.org/0009-0002-5133-5399, https://orcid.org/0009-0003-3895-1215, https://orcid.org/0009-0002-4330-4154, https://orcid.org/0000-0002-1366-4389, https://orcid.org/0000-0002-2826-5444

[a]*Department of Plant Protection, Faculty of Agriculture, Universitas Gadjah Mada, 55281 Sleman, Indonesia*

[b]*Department of Plant Protection, Faculty of Agriculture, Bilecik Şeyh Edebali University, Bilecik, 11230, Türkiye*

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*Corresponding author: Adyatma Irawan SANTOSA

adyatma.i.s@ugm.ac.id

ABSTRACT

Begomoviruses are significant plant pathogens affecting various crops globally. Furthermore, weeds serve as reservoirs for these viruses, contributing to their spread and persistence. Field surveys in Sleman and Gunungkidul Regencies in Special Region of Yogyakarta, Indonesia, collected four *Acalypha indica* L. samples showing leaf cupping, mosaic, and stunting, and two *Euphorbia heterophylla* L. samples exhibiting chlorosis, mosaic, and stunting. Molecular detection and phylogenetic analysis revealed the presence of ageratum yellow vein China virus (AYVCNV) in all six samples based on the sequences of the partial AV1 gene. However, SPG1/SPG2 primers also showed that three isolates (katemas SMN1, katemas SMN2, and akar kucing SMN2) had recombinant sequences in the partial AC1-AC2 regions, with Ageratum yellow vein virus (AYVV) as one of the parent strains, indicating genetic exchange between both *Begomovirus* species. A scan using the Recombination Detection Program (RDP v5.30) confirmed strong signals in the three isolates, supporting the role of recombination in the evolution of begomoviruses. Two A. indica samples with systemic yellow vein clearing were also collected but tested negative using both primer pairs, indicating a different disturbance affecting them. This study molecularly characterized AYVCNV infecting *A. indica* and *E. heterophylla* for the first time in Indonesia and elsewhere. The findings highlight the importance of these widely distributed tropical weeds as alternative hosts for begomoviruses and underscore the need for continued monitoring to manage these viruses effectively in agricultural settings effectively.

INTRODUCTION

In recent years, begomoviruses have emerged as major problems in tropical agriculture. These viruses, whose genome is circular single-stranded DNA and are transmitted by whiteflies (*Bemisia tabaci*), have been documented to infect a range of host plants, including economically important crops and various weeds (Fiallo-Olivé et al.

2021, Krishna Reddy et al. 2024). Similarly, the spread of begomoviruses in agricultural and natural ecosystems is a growing concern in Indonesia (Santosa et al. 2024, Wahyono et al. 2023). Previous studies have documented the occurrence of Tomato leaf curl New Delhi virus (ToLCNDV), Pepper yellow leaf curl Indonesia virus (PepYLCIV), Mungbean yellow mosaic India virus (MYMIV), Squash leaf curl China virus (SLCCNV), and Ageratum yellow vein China virus (AYVCNV) in various regions within the country, with detection in both cultivated crops and weed species such as *Ageratum conyzoides* and *Amaranthus spinosus* (Santosa and Somowiyarjo 2023, Taufik et al. 2024). The presence of plant viruses in commonly found weeds is particularly concerning, as it highlights the role of alternative hosts as sources of viral inoculum, which can influence their epidemiology of begomoviruses in major crops (Çelik and Santosa 2024, Maliano et al. 2021).

Acalypha indica and *Euphorbia heterophylla* are two weed species from the family *Euphorbiaceae* that are widely distributed across tropical and subtropical regions. They play damaging roles in agricultural ecosystems, not only competing for space and nutrients with main crops but also by hosting various plant pathogens, particularly begomoviruses. *A. indica* has been shown to be susceptible to Tomato leaf curl virus (ToLCV) in India (Mall et al. 2014) and Mungbean yellow mosaic virus (MYMV) in Indonesia (Sidik et al. 2022). Meanwhile, Euphorbia mosaic virus (EuMV) has been detected in *E. heterophylla* and passionfruit (*Passiflora edulis*) growing near the weed in Florida, USA, with both plant species exhibited severe symptoms (Polston et al. 2017). However, the capacity of *A. indica* and *E. heterophylla* as potential reservoirs for begomoviruses has not been thoroughly investigated, making it a critical area of research.

The DNA-A molecule of bipartite begomoviruses shares a similar genomic structure with that of monopartite begomoviruses (Stanley et al. 2005). Due to their small genome size (~2.7 kb), begomoviruses encode only a limited number of proteins that perform various virulence-related roles (Shafiq et al. 2023). Typically, the DNA-A component of both mono- and bipartite begomoviruses encodes six essential proteins responsible for viral replication, movement, and gene expression regulation. Of these, two open reading frames (ORFs), V1 and V2, are located on the virion (V) strand, while four ORFs (C1–C4) are found on the complementary (C) strand. ORF V1 codes for the coat protein (CP), V2 for the pre-coat protein, C1 encodes the replication-associated protein (Rep), C2 codes for the transcriptional activation protein (TrAP), C3 encodes the replication enhancer protein (REn), and C4 encodes the C4 protein, which typically acts as a pathogenicity determinant (Shafiq et al. 2023).

The molecular characterization of begomoviruses involves analyzing their genome sequences to identify specific genetic markers that can be used for their identification and classification. This approach is essential for understanding the genetic diversity of begomoviruses, their evolutionary relationships, and their mechanisms of pathogenicity (Nigam 2021). The main objective of this study is to perform molecular characterization of partial AV1 (involved in transmission facilitated by whiteflies and the assembly of the virion capsid), AC1 (responsible for viral DNA replication), and AC2 (a transcriptional activator regulating the expression of virus-sense genes) genes of begomoviruses present in *A. indica* and *E. heterophylla* weeds from Indonesia and to reveal their genetic diversity. This study will also provide valuable insights into the role of weeds as reservoirs of plant viruses and their potential impact on local agriculture, informing future efforts to manage begomovirus-related diseases in Indonesia and other regions where these viruses are prevalent.

MATERIALS AND METHODS

Sampling and location

During field expeditions from June to July 2024, leaves of *A. indica* and *E. heterophylla* exhibiting clear symptoms of begomovirus infection were collected from Sleman and Gunungkidul Regencies, Special Region of Yogyakarta, Indonesia. Non-symptomatic samples were also collected from the same locations. The samples were intentionally selected and then transported to the Phytopathology Laboratory at Universitas Gadjah Mada, where they were stored at -20 °C for subsequent analysis.

DNA extraction and PCR

Genomic DNA was extracted from each collected sample using the DNA extraction Mini Kit for Plants, following the standard protocol provided by Geneaid Biotech Ltd. (Taiwan). PCR was performed twice for each sample using two universal primer pairs to detect begomoviruses: Krusty (F 5`-CCNMRDGGHTGTGARGGNCC-3`)/Homer (R 5`-SVDGCRTGVGTRCANGCCAT-3`) (KH), targeting approximately 530 bp of the partial AV1 gene (Revill et al. 2003), and SPG1 (F 5`-CCCCKGTGCGWRAATCCAT-3`)/ SPG2 (R 5`-ATCCVAAYWTYCAGGGAGCT-3`) (SPG), amplifying about 900 bp of the partial AC1 and AC2 genes (Li et al. 2004).

Each PCR reaction was prepared in a 40 µl volume, consisting of 2 µl of each primer (10 pmol/µl), 20 µl of MyTaq HS Red Mix (Bioline, Germany), 4 µl of DNA template, and 12 µl

of PCR-grade water. The PCR cycling conditions were as follows: pre-denaturation at 96 °C for 3 minutes, followed by 35 cycles of denaturation at 96 °C for 1 minute, annealing at 55 °C for KH and 59 °C for SPG for 1 minute, extension at 72 °C for 1 minute, and a final extension at 72 °C for 10 minutes.

The resulting PCR products were loaded onto agarose gels stained with Florosafe DNA Staining (1st BASE, Malaysia) and subjected to electrophoresis at 50 V for 50 minutes. PCR bands were visualized and measured under a UV transilluminator (Optima Inc., Japan). Successfully amplified products were sent to Integrated Research and Testing Laboratory (LPPT) at Universitas Gadjah Mada for bidirectional Sanger sequencing to determine the nucleotide sequences of partial AV1, AC1, and AC2 genes for each isolate. Species identification of the isolates was achieved using the online nucleotide BLAST tool (https://blast.ncbi.nlm.nih.gov), which compared the newly obtained sequences with those in the NCBI GenBank database. The sequences of the new isolates were subsequently submitted to GenBank to obtain unique accession numbers.

Phylogenetic study

Complete genome sequences of begomovirus isolates registered in GenBank were aligned and trimmed to match the lengths of the newly obtained sequences using the ClustalW algorithm in MEGA11 software (Tamura et al. 2021). Two phylogenetic trees — one for the partial AV1 gene and another for the partial AC1 and AC2 genes—were then constructed using the Maximum Likelihood (ML) method with the Tamura-Nei model (Tamura and Nei 1993) in MEGA11. The statistical significance of each branch was assessed through 1,000 bootstrap replicates.

Recombination analysis

Possible recombination events within the genomes of isolates placed in different species groups in the constructed phylogenetic trees were analyzed using the Recombination Detection Program (RDP v.5.30) (Martin et al. 2020). An event was considered credible only if it was identified by at least five of the algorithms (Bootscan, MaxChi, Chimaera, 3Seq, Siscan, GENECONV, and RDP) included in the software, with a Bonferroni-corrected p-value of less than 0.05 indicating statistical significance (Martin et al. 2020).

RESULTS

Field surveys and molecular identification

Leaves from seven *A. indica* and three *E. heterophylla* plants were collected from Sleman and Gunungkidul Regencies, Special Region of Yogyakarta, Indonesia. Four *A. indica* samples exhibiting leaf cupping, mosaic, and stunting, as well as two *E. heterophylla* samples showing chlorosis, mosaic, and stunting, tested positive for begomovirus infection. Meanwhile, two *A. indica* plants with systemic vein clearing, along with asymptomatic *A. indica* and *E. heterophylla* samples, tested negative (Figure 1).

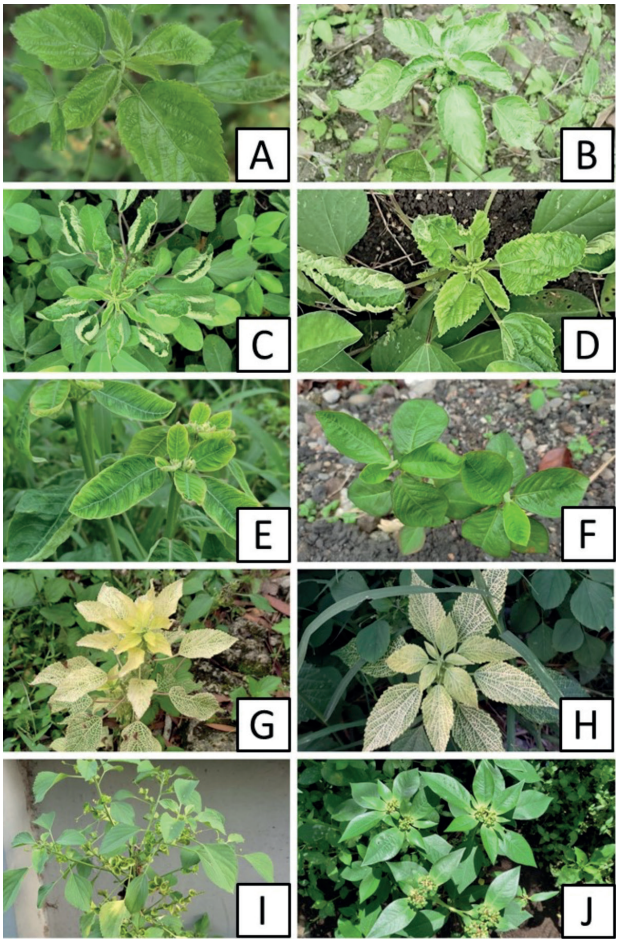

Figure 1. The ten samples tested in this report: A) *Acalypha indica* with mosaic and leaf cupping from Sleman Regency infected by akar kucing SMN1 isolate, B) *A. indica* with mild leaf cupping from Sleman Regency infected by akar kucing SMN2 isolate, C) *A. indica* with severe leaf cupping from Gunungkidul Regency infected by akar kucing GK1 isolate, D) *A. indica* with severe leaf cupping and stunting from Gunungkidul Regency infected by akar kucing GK2 isolate, E) *Euphorbia heterophylla* with mosaic and leaf cupping from Sleman Regency infected by katemas SMN1 isolate, F) *E. heterophylla* with leaf cupping and stunting from Sleman Regency infected by katemas SMN2 isolate, G) *A. indica* sample akar kucing SMN3 with severe vein clearing from Sleman Regency tested negative, H) *A. indica* sample akar kucing SMN4 with severe vein clearing from Sleman Regency tested negative, I) *A. indica* sample akar kucing SMN5 without symptoms from Sleman Regency tested negative, J) *E. heterophylla* sample katemas SMN3 without symptoms from Sleman Regency tested negative

BLAST analysis of the partial AV1 gene sequences obtained using KH primer pair revealed that all six isolates were identified as Ageratum yellow vein China virus (AYVCNV). Meanwhile, sequences obtained using SPG primer pair demonstrated that the katemas SMN1, katemas SMN2, and akar kucing SMN2 isolates had the highest identity to Ageratum yellow vein virus (AYVV). GenBank accession numbers PQ368889- PQ368894 were assigned to the partial AV1 gene sequences, while PQ368895- PQ368900 were assigned to the partial AC1 and AC2 gene sequences (Table 1).

Table 1. Isolates of begomoviruses identified in this study

No	Isolate Name	Species[α]	Host	Origin	Genbank Accession No.	
					Partial AV1 gene	Partial AC1 and AC2 genes
1	katemas SMN1	AYVCNV/AYVV[β]	*Euphorbia heterophylla*	Sleman	PQ368889	PQ368895
2	katemas SMN2	AYVCNV/AYVV[β]	*Euphorbia heterophylla*	Sleman	PQ368890	PQ368896
3	akar kucing SMN1	AYVCNV	*Acalypha indica*	Sleman	PQ368891	PQ368897
4	akar kucing SMN2	AYVCNV/AYVV[β]	*Acalypha indica*	Sleman	PQ368892	PQ368898
5	akar kucing GK1	AYVCNV	*Acalypha indica*	Gunungkidul	PQ368893	PQ368899
6	akar kucing GK2	AYVCNV	*Acalypha indica*	Gunungkidul	PQ368894	PQ368900

[α] ageratum yellow vein China virus = AYVCNV, ageratum yellow vein virus= AYVV.
[β] Recombinant isolates.

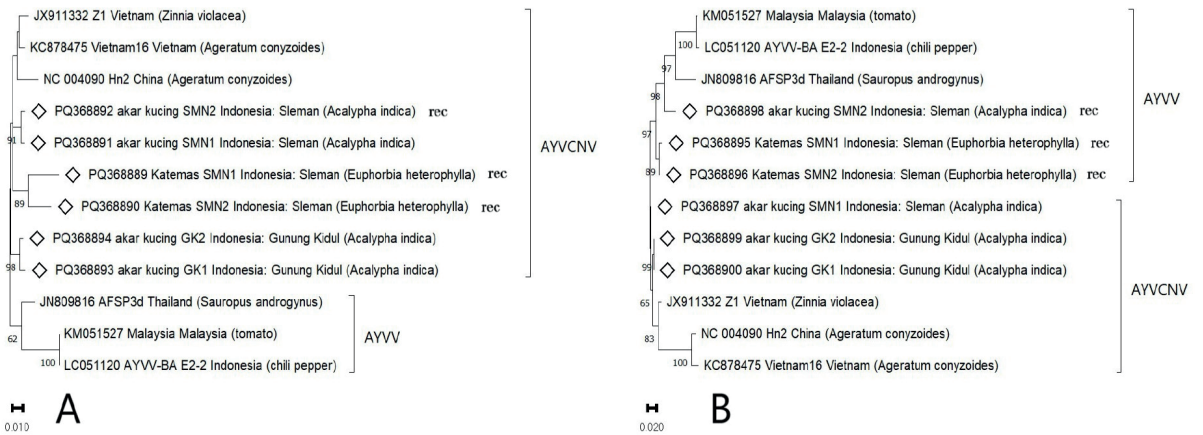

Figure 2. Phylogenetic trees constructed using MEGA11 software. A. Based on 518 nt partial sequences of the AV1 gene obtained using the KH primer pair, B. Based on 893 nt partial sequences of AC1-AC2 genes obtained using SPG1 primer pair. AYVCNV and AYVV recombinant isolates were marked with 'rec'. AYVCNV = ageratum yellow vein China virus, AYVV = ageratum yellow vein virus

Phylogenetic trees

Phylogenetic analysis of the partial AV1 sequences showed that all the four *A. indica* and two *E. heterophylla* isolates clustered within the AYVCNV reference isolates. However, the AC1-AC2 regions of the katemas SMN1, katemas SMN2, and akar kucing SMN2 isolates were grouped with AYVV, while the other three isolates clustered with AYVCNV (Figure 2). This suggests the possibility of a recombination event within the genomes of katemas SMN1, katemas SMN2, and akar kucing SMN2 isolates, necessitating further recombination analysis using specialized software.

Recombination events

Recombination analysis using the RDP software revealed potential recombination events in the AC1-AC2 regions of the katemas SMN1, katemas SMN2, and akar kucing SMN2 isolates from Sleman Regency. These events showed strong signals, detectable by all seven algorithms (Table 2). The analysis also suggested that an AYVV isolate from Malaysia (GeneBank accession no. KM051527) might be the major parent, while their minor parent could be an AYVCNV isolate from Vietnam (GenBank accession no. KC878475).

Table 2. Putative recombination events detected in the partial AC1 and AC2 genes of isolates analyzed in this study using RDP v5.30

No.	Recombinant Isolate	Major/ Minor Parents	RDP Implemented Method[2] (*p* Value)
1	katemas SMN1	AYVV KM051527/ AYVCNV KC878475	R (1.445×10^{-8}) G (2.515×10^{-6}) B (3.212×10^{-12}) M (1.303×10^{-12}) C (1.632×10^{-10}) S (4.774×10^{-10}) 3S (2.451×10^{-13})
2	katemas SMN2	AYVV KM051527/ AYVCNV KC878475	R (1.599×10^{-7}) G (3.237×10^{-12}) B (2.556×10^{-10}) M (2.911×10^{-11}) C (3.661×10^{-9}) S (5.723×10^{-9}) 3S (4.521×10^{-23})
3	akar kucing SMN2	AYVV KM051527/ AYVCNV KC878475	R (1.238×10^{-15}) G (3.433×10^{-16}) B (5.111×10^{-15}) M (2.142×10^{-20}) C (1.364×10^{-18}) S (5.773×10^{-15}) 3S (1.537×10^{-11})

DISCUSSION

Begomoviruses are particularly concerning due to their ability to cause severe diseases in a wide range of crops (Fiallo-Olivé and Navas-Castillo 2023). Previously, the occurrence of begomoviruses such as ToLCV and MYMV in *A. indica*, and EuMV in *E. heterophylla* had been documented in various regions worldwide (Mall et al. 2014, Polston et al. 2017, Sidik et al. 2022). The detection of AYVCNV in *A. indica* and *E. heterophylla* adds to the growing body of evidence that these and other weeds can serve as significant reservoirs for begomoviruses, which may subsequently infect economically important crops.

The four *A. indica* samples infected by AYVCNV exhibited distinctive leaf cupping symptoms. Two *A. indica* samples with conspicuous systemic vein clearing (Figure 1), collected in two different regions within Sleman Regency, tested negative for begomovirus, indicating that this specific abnormality might be associated with other pathogens or abiotic factors that require further investigation.

AYVCNV has been reported in *A. conyzoides* in China and Indonesia (Santosa and Somowiyarjo 2023, Xiong et al. 2007), as well as in ornamentals and weeds such as *Zinnia elegans* in Vietnam (Li et al. 2013), *Synedrella nodiflora* in the Philippines (She et al. 2015), *Sonchus oleraceus* in China (Mo et al. 2023), and *A. spinosus* in Indonesia (Santosa and Somowiyarjo 2023). Meanwhile, AYVV has been found infecting *A. conyzoides* in Southeast Asian countries, including Indonesia and Singapore (Kon et al. 2007, Saunders et al. 2000, Tan et al. 1995). More recent findings have identified main crops as hosts for AYVV, including papaya (*Carica papaya*) in Nepal and Indonesia (Helina et al. 2024, Shahid et al. 2013), and common bean (*Phaseolus vulgaris*) in Japan (Tomitaka et al. 2020) as hosts of AYVV. These results highlight the importance of monitoring alternative hosts for begomoviruses, particularly in regions where these viruses are prevalent.

The phylogenetic analysis revealed an intriguing finding: the katemas SMN1, katemas SMN2, and akar kucing SMN2 isolates from Sleman clustered with AYVCNV in the partial AV1 region but grouped with AYVV in the partial AC1-AC2 regions. This discrepancy suggests recombination events, where segments of the virus genome from different parent strains combined to form a new recombinant virus. Recombination is a well-documented phenomenon in begomoviruses and plays a crucial role in their evolution, potentially leading to the emergence of new viral strains with altered virulence or expanded host ranges (Padidam et al. 1999).

Strong signals of the recombination were detected in all three isolates using all seven algorithms in the RDP analysis. This may indicate that the recombinant segments

are relatively long or that the recombination event occurred relatively long ago, leading to high sequence divergence between the parental and recombinant strains (Martin et al. 2020). In agreement with these results, the phylogenetic analysis clearly indicated that the AC1-AC2 regions of the isolates were more closely related to AYVV than AYVCNV, suggesting they were inherited from AYVV strains. Understanding the molecular characteristics of AYVV and AYVCNV in *A. indica* and *E. heterophylla* will provide valuable insights into their epidemiology and the potential risks they pose to surrounding agricultural systems (Maliano et al. 2021).

Recombination in plant viruses, particularly in begomoviruses, is a critical factor in the evolution of virulence and adaptability. Recombinant viruses can acquire new characteristics, such as increased virulence, expanded host range, or resistance to plant defenses, making them more challenging to manage (Duffy and Holmes 2008). The recombinant nature of the three isolates highlights the ongoing genetic exchanges occurring in the begomovirus population in Indonesia and suggests that continuous monitoring and genetic characterization of these viruses are essential for understanding their epidemiology and developing effective control strategies.

This study provides valuable insights into the occurrence and molecular characteristics of begomoviruses in two important weeds in the Tropics and Subtropics: *A. indica* and *E. heterophylla*. The detection of AYVCNV in these weed species, along with evidence of recombination in three isolates, underscores the importance of weeds as reservoirs and sources of genetic diversity for begomoviruses. The findings emphasize the need for monitoring and managing begomoviruses in both crops and weeds to mitigate the potential spread and evolution of highly virulent strains.

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Author's Contribution

A.S. conducted laboratory work, reviewed the literature, and wrote the draft manuscript; U.N., D.P.N, and N.V. collected samples and assisted in laboratory work. F.R-Z. revised the original manuscript. A.I.S. designed and supervised the research, analyzed data, and revised the original manuscript.

Statement of Conflict of Interest

The authors have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

ÖZET

Begomovirüsler, dünya genelinde tarımsal üretimi tehdit eden önemli bitki patojenleridir. Bununla birlikte, yabancı otlar bu virüsler için alternatif konukçu olarak işlev görmekte ve virüslerin yayılımı ile kalıcılığına katkıda bulunmaktadır. Bu çalışmada, Endonezya'nın Yogyakarta Özel Bölgesi'nde yer alan Sleman ve Gunungkidul bölgelerinde yürütülen arazi araştırmaları kapsamında, *Acalypha indica* L. bitkisinden dört, *Euphorbia heterophylla* L. bitkisinden ise iki simptomatik örnek toplanmıştır. Moleküler analizler sonucunda, AV1 gen bölgesine ait kısmi diziler kullanılarak tüm örneklerde Ageratum yellow vein china virus (AYVCNV) varlığı tespit edilmiştir. Ancak, SPG1/SPG2 primerleri ile gerçekleştirilen analizlerde, üç izolatın (katemas SMN1, katemas SMN2 ve akar kucing SMN2) AC1-AC2 gen bölgelerinde rekombinant dizilere sahip olduğu belirlenmiş olup, filogenetik analizler bu bölgelerin Ageratum yellow vein virus (AYVV) ile yüksek benzerlik gösterdiğini ortaya koymuştur. Rekombinasyon Saptama Programı (RDP v5.30) ile yapılan analizler, bu üç izolatın güçlü rekombinasyon sinyalleri verdiğini doğrulamış ve rekombinasyonun begomovirüslerin evriminde önemli bir rol oynadığına işaret etmiştir. Ek olarak, sistemik damar açılması simptomu gösteren iki *A. indica* örneği de değerlendirilmiş ancak moleküler analizlerde begomovirüs varlığı tespit edilmemiştir; bu durum, farklı bir patojen ya da abiyotik stres faktörünün etkili olabileceğini düşündürmektedir. Bu çalışma, AYVCNV'nin *A. indica* ve *E. heterophylla* konukçularında enfeksiyon oluşturduğunu ilk kez moleküler düzeyde tanımlamakta ve bu virüslerin genetik çeşitliliği ile evrimsel dinamiklerine dair önemli veriler sunmaktadır. Elde edilen bulgular, tropikal ve subtropikal bölgelerde yaygın olarak bulunan bu yabancı ot türlerinin begomovirüsler için önemli rezervuarlar olduğunu göstermekte ve virüslerin yayılımını önlemeye yönelik izleme ve yönetim stratejilerinin geliştirilmesi gerekliliğini vurgulamaktadır.

Anahtar kelimeler: DNA virüs, genetik rekombinasyon, filogenetik ağaç, Polimeraz Zincir Reaksiyonu, alternatif bitki konukçusu.

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