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Genetic Diversity and Evolutionary Dynamics of Begomoviruses Reported from Sri Lanka

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ABSTRACT

Begomoviruses, members of the family *Geminiviridae*, pose a major challenge to crop production in Sri Lanka and globally due to their extensive host range and high evolutionary potential. This study investigated the genetic diversity and evolutionary dynamics of begomoviruses reported from Sri Lanka using publicly available genomic sequences. Viral sequences were retrieved from the NCBI database and aligned using MUSCLE. Pairwise sequence identity was assessed using SDT (v1.2), while phylogenetic relationships, nucleotide diversity, and selection pressure analyses were conducted using MEGA version 12. Recombination events were detected using RDP4 employing multiple algorithms. The analysis revealed four major begomovirus groups based on sequence identity and phylogenetic clustering: *Okra enation leaf curl virus* (OELCuV), *Bhendi yellow vein mosaic virus* (BYVMV), *Sri Lankan cassava mosaic virus* (SLCMV), and *Tomato leaf curl Sri Lankan virus* (ToLCSLV). Phylogenetic analysis supported clear species level segregation with strong bootstrap confidence. Five recombination events were identified, indicating active genetic exchange among begomovirus populations. Selection pressure analysis showed that most viral genes are under strong purifying selection, suggesting evolutionary conservation, whereas limited evidence of positive selection was observed in specific genes. Nucleotide diversity varied among populations, with OELCuV isolates exhibiting the lowest diversity, indicating a more conserved genome compared to other groups. Overall, this study highlights the significant genetic diversity and ongoing evolution of begomoviruses in Sri Lanka, emphasizing the role of recombination and selection in shaping viral populations and their potential impact on crop health and management strategies.

Keywords: Begomovirus, Recombination, Phylogenetic tree, Nucleotide diversity and Purifying selection.

1. INTRODUCTION

Begomovirus is the most important genus becomes under the family Geminiviridae, transmitted by whitefly known as *Bemisia tabaci*. It causes major threat to many dicotyledonous plants [1,2] including tomato, cotton, cassava, beans and ornamentals [3]. *Begomovirus* have monopartite or bipartite genomes. Bipartite *begomovirus* genomes consist of two ssDNA molecules namely DNA-A and DNA-B which are equal in size (2.8 kb) [4]. The DNA-A genome has five or six open reading frames (ORFs). Viral sense strand code for coat protein (CP) and pre – coat protein (Pre-CP). Replication- associated protein (Rep), Replication enhancer protein (Ren), Transcriptional activator protein (TrAP) and AC4 protein coded in the complementary sense strand [5]. The DNA-B genome consist two ORFs such as: BV1 and BC1, they code for nuclear shuttle protein (NSP) and movement protein (MP), respectively [6,7]. Circular, single-stranded DNA molecules size varies from 1.3 kb to 1.5 kb known as betasatellite. Betasatellite molecules consist of a single conserved ORF which encode βC1, whereas, some recent reports suggest it also has another ORF, called βV1[8]. Betasatellite molecules help to determine the symptom development in host plants as well as suppression of transcriptional and post

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transcriptional gene silencing even though these molecules are considered as an associated DNA particle in *begomovirus* genome complex [9]. The alphasatellites produce their own replication-associated protein but rely on the helper virus for encapsidation, movement and transcription [10,7]. These alphasatellites reduce the severity of disease symptoms and help to keep the accumulation of betasatellite at low level. Both alpha and betasatellites are linked with monopartite old world *begomovirus*. Coding capacity is lack in deltasatellites. Size of the deltasatellite is about one-quarter of the *begomovirus* genome component. In certain instances, deltasatellites either decrease or increase the replication of the helper *begomovirus*, but they seldom alter the symptoms produced by it [2,7].

Begomoviruses have become major constraints to the cultivation of many crops across different regions of the world. Several diseases caused by these viruses are highly destructive. The increasing emergence of new *begomoviruses* indicates that they continue to evolve and represent a significant threat to sustainable agriculture, especially in tropical and subtropical regions. In recent years, some *begomoviruses* have also spread to temperate areas, raising concerns for vegetable production in greenhouses. Another worrying development is the appearance of diseases involving complexes of *Begomoviruses* and associated satellite DNA molecules [11].

Begomovirus outbreaks are significant and continuing agricultural problem in Sri Lanka, causing considerable yield losses in major crops such as chilli, okra, cassava, tomato and bean. Seven different *begomoviruses* have been reported such as; *Bhendi Yellow Vein Mosaic Virus* (Accession No- MH455209-MH455212, KX698089, MT572475-MT572477) , *Chilli Leaf Curl Virus* (JN555600, NC-055131), *Tomato Leaf Curl Sri Lankan Virus* (AF274349, PP935246-PP935252), *Horsegram Yellow Mosaic Virus* (GU323321), *Okra Enation Leaf* Curl Virus (KX698093, KX698087, KX698092, MH455207, MH455208, MN389529, MN384976), Cassava Mosaic Virus (AJ314737, OK377341-OK377343, OK362288, OK424595) and *Ageratum yellow vein Sri Lanka virus*(NC-002981) (https://www.ncbi.nlm.nih.gov/).

Genetic variation arising from mutation, recombination, and pseudo recombination contributes to the evolution of *begomoviruses* [12]**.** In Sri Lanka, although viral diseases significantly impact on crop production, comprehensive studies on *begomoviruses* are limited. Virus identification relies on genome analysis, but few complete *begomovirus* genomes from Sri Lanka are available, and their genetic diversity remains poorly studied. There is a need for comparative genomic and phylogenetic analysis to understand the diversity and evolutionary relationships of Sri Lankan *begomoviruses*.

2. MATERIALS AND METHODOLOGY

2.1 Source of virus sequences

Begomovirus sequences reported from Sri Lanka (Table 1) were retrieved from the National Center for Biotechnology Information (NCBI) (https://www.ncbi.nlm.nih.gov) database..

2.2 Genome characterization and pairwise sequence identity analysis

The characteristics of complete genome of *begomovirus* was analyzed using CLC Sequence Viewer (v8). Multiple sequence alignment was performed using Multiple Sequence Comparison by Log Expectation (MUSCLE) tool [13] in MEGA 12 software. Pairwise identity score was calculated using Sequence Demarcation Tool SDT (v1.2) [14].

2.3 Phylogenetic analysis

Phylogenetic trees were constructed using Neighbor-joining (NJ) method in MEGA 12 software [15] using P-distance nucleotide substitution model. Bootstrap analysis with 1000 replicates was performed to estimate the confidence values.

2.4 Recombination analysis

Possible recombination events were examined using sequences obtained from the GenBank database. Identification of potential recombinant sequences, probable parental isolates, and

recombination breakpoints was conducted by the RDP, GENECONV, BootScan, MaxChi, Chimaera, SiScan, and 3Seq methods incorporated in the Recombination Detection Program (RDP) version 4 [16]. The analysis was performed under default parameters, applying a 0.05p- value threshold with standard Bonferroni corrections throughout [1,17].

2.5 Selection pressure analysis

Multiple sequence alignment was performed using MEGA 12 software for the *begomovirus* gene sequences. Codon based Z test was selected. The values of nonsynonymous substitution rate (dN) and synonymous substitution rate (dS) were assessed using the Pamilo-Bianchi-Li method in MEGA 12 [17]. The pattern of selection was inferred using the ratio of non-synonymous to synonymous nucleotide substitution rates (dN/dS). Corresponding to negative selection (dN/dS<1), neutral evolution (dN/dS=1) or positive selection (dN/dS>1).

2.6 Nucleotide diversity analysis

Nucleotide diversity estimates the average pairwise differences among sequences [17]. Each Populations (Eg: Population 1, Population 2 etc.) were defined in MEGA 12 Software. Average nucleotide diversity was estimated for each population as well as entire population.

3. RESULTS AND DISCUSSION

Begomoviruses are the most significant plant viruses due to their widespread distribution and impact on crop productivity. The present study focused on characterization of begomoviruses reported from Sri Lanka, analyzing their genetic variation, recombination, selection pressure, and nucleotide diversity. Seven different *begomovirus* species were identified from Sri Lanka, namely *Ageratum yellow vein Sri Lanka virus* (AYVSLV), *Chilli leaf curl virus* (ChLCV), *Horsegram yellow mosaic virus* (HgYMV), *Okra enation leaf curl virus* (OELCuV), *Bhendi yellow vein mosaic virus* (BYVMV), *Sri Lankan cassava mosaic virus* (SLCMV), and *Tomato leaf curl virus* (ToLCV).

3.1 Characterization of complete genome of begomoviruses reported from Sri Lanka.

The results of the complete genome sequence analysis performed using CLC Sequence Viewer (Version 8) are presented in Table 2. The sequences used for this analysis were retrieved from the NCBI database. For each *begomovirus* isolate reported from Sri Lanka, sequence type, length, single-strand molecular weight, and C+G, A+T composition frequencies were examined. Most sequences had lengths ranging between 2735 and 2762 bp. Multiple sequence alignment indicated the presence of both conserved and hypervariable regions, suggesting adaptive evolution in response to different host plants and environmental conditions.

3.2 Pairwise identity analysis

Pairwise analysis based on International Committee on Taxonomy of Viruses (ICTV) Demarcation Thresholds; For *begomoviruses*, if the pairwise identity is less than 91%, they are different species. If the pair wise identity is greater than 94%, they are same species with same strain. If the pairwise identity is greater than 91% but less than 94%, they are different strain of a species. So, based on this, four prominent groups were observed. First group was *Okra Enation Leaf Curl Virus* (OELCuV), Second group was *Bhendi Yellow Vein Mosaic Virus* (BYVMV), Third group was *Tomato Leaf Curl Sri Lankan Virus* (ToLCSLV) and fourth group was *Sri Lankan Cassava Mosaic Virus* (SLCMV) (Figure 1). These findings were further supported by phylogenetic tree analysis.

3.3 Phylogenetic tree analysis

Phylogenetic analysis of the DNA-A sequences revealed the formation of four well-supported clades corresponding to OELCuV, BYVMV, ToLCSLV, and SLCMV. The majority of isolates grouped within the OELCuV cluster, forming a distinct and strongly supported lineage, indicating high genetic similarity among these sequences. A separate, moderately supported clade represented BYVMV, clearly differentiated from the OELCuV group.

Table 1. Begomoviruses reported from Sri Lanka

Host	Virus	Abbreviation	Accession no
Okra (*Abelmoschus esculentus)*	*Okra enation leaf curl virus*	OELCuV(LK:Tri:15)	KX698087
		OELCuV(LK:Jaf:15)	KX698088
		OELCuV(LK:Vav:15)	KX698090
		OELCuV(LK:Put:15)	KX698091
		OELCuV(LK:Mat:15)	KX698092
		OELCuV(LK:TrO2:15)	MH455207
		OELCuV(LK:VaO2:15)	MH455208
		OELCuV(LK:Bat:15)	KX698093
		OELCuV(SL:DAVaO2:18)	MN389529
		OELCuV(SL:DAJf01:18)	MN384976
Ageratum conyzoides	*Ageratum yellow vein Sri Lanka virus*	AYVSLV(LK:99)	NC-002981
Bean (*Phaseolus vulgaris*)	*Horsegram yellow mosaic virus*	HgYMV (LK:09)	GU323321
Okra (*Abelmoschus esculentus)*	*Bhendi yellow vein mosaic virus*	OYVMV(SL:Ang:20)	MT572477
		BYVMV(LK:JaO2:15)	MH455209
		BYVMV(LK:Kan:15)	KX698089
		BYVMV(LK:KaO2:15)	MH455210
		BYVMV(LK:PuO2:15)	MH455211
		BYVMV(LK:MaO2:15)	MH455212
		OYVMV(SL:Mah:20)	MT572476
		OYVMV(SL:Gan:20)	MT572475
Chilli (*Capsicum annuum)*	*Chilli leaf curl virus*	ChLCV(LK:Noc:09)	JN555600
		ChLCV(SL:CL14:09)	NC-055131
Cassava (*Manihot esculenta)*	*Sri Lankan cassava mosaic virus*	SLCMV(LK:Col:98)	AJ314737
		SLCMV(SL:Kin:21)	OK377342
		SLCMV(SL:Pd:21)	OK362288
		SLCMV(SL:Mut:21)	OK424595
		SLCMV(SL:Kuc:21)	OK377343
		SLCMV(SL:Nil:21)	OK377341
Tomato (*Solanum lycopersicum)*	*Tomato leaf curl Sri Lankan virus*	ToLCSLV(LK:Ban:97)	AF274349
		ToLCSLV(LK:TKO6:20)	PP935246
		ToLCSLV(LK:TKO4:20)	PP935248
		ToLCSLV(LK:TKaO4:20)	PP935251
		ToLCSLV(LK:TJO2:20)	PP935252
	Tomato leaf curl Bangalore virus	ToLCBV(SL:TJO3:20)	PP935247
	Tomato leaf curl Karnataka virus	ToLCKV(SL:TJ12:20)	PP935249
		ToLCKV(SL:TMtO5:20)	PP935250

Table 2. Complete genome characteristics of Begomoviruses reported from Sri Lanka

Virus name	Sequence type	Length (bp)	Single-strand Weight (kDa)	A+T (frequency)	C+G (frequency)
OELCuV(LK:VaO2:15)	DNA	2738	846.856	0.564	0.436
OELCuV(LK:DAJfn01:15)	DNA	2738	846.784	0.564	0.436
BYVMV(LK:Kan:15)	DNA	2786	862.407	0.563	0.437
BYVMV(LK:JaO2:15)	DNA	2749	850.980	0.569	0.428
SLCMV(LK:Col:98)	DNA	2755	851.621	0.574	0.466
SLCMV(SL:Pd:21)	DNA	2746	848.637	0.539	0.461
SLCMV(SL:Kuc:21)	DNA	2746	846.635	0.538	0.462
OELCuV(LK:Tri:15)	DNA	2738	846.815	0.562	0.438
SLCMV(SL:Nil:21)	DNA	2746	848.644	0.538	0.462
BYVMV(LK:PuO2:15)	DNA	2735	846.319	0.568	0.432
SLCMV(LK:Mut:21)	DNA	2746	848.742	0.539	0.461
AYVSLV(LK:99)	DNA	2748	850.240	0.574	0.426
OELCuV(LK:DAVavO2:18)	DNA	2741	847.960	0.564	0.451
OELCuV(LK:Bat:15)	DNA	2738	846.661	0.562	0.438
OELCuV(LK:Vav:15)	DNA	2738	846.816	0.564	0.436
HgYMV(LK:09)	DNA	2735	845.472	0.558	0.442
OELCuV(LK:TrO2:15)	DNA	2762	854.465	0.562	0.438

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The ToLCSLV and SLCMV isolates formed independent clusters with high bootstrap support, confirming their genetic distinctness. Overall, the tree topology demonstrates clear species-level segregation among begomoviruses, with strong bootstrap values supporting the reliability of the inferred phylogenetic relationships. (Figure 2)

3.4 Recombination analysis

In RDP4, each letter is stand for; R-RDP, G-GeneConv, B-Bootscan, M-MaxChi, C-Chimera and S-SisScan. The reported P values are for the methods by underline, and they are the lowest P values calculated for the regions in question.

Recombination analysis of full-length DNA-A sequences using RDP4 revealed five potential recombination events among begomoviruses reported from Sri Lanka (Table 3). These events involved several virus species, including ChLCV, ToLCBV, AYVSLV, OELCuV, ToLCSLV, BYVMV, and SLCMV, suggesting active genetic exchange among viruses present in the field. It provides strong evidence that recombination acts as a key mechanism driving begomovirus evolution. Which is confirmed by Padidam *et al*., and Lefeuvre and Moriones [18, 19], who demonstrated that recombination facilitates the emergence of new begomovirus strains with altered virulence and host adaptation. Most of the detected events were strongly supported, with very low p-values and confirmation by multiple detection methods. In some cases, one of the parental sequences could not be identified, indicating the possible involvement of uncharacterized or unsampled viral variants. Overall, the results underscore the significant role of recombination in generating genetic diversity among begomoviruses in Sri Lanka.

3.5 Selection pressure analysis

Selection pressure analysis of begomovirus gene sequences from Sri Lanka revealed that most genes were evolving under purifying selection. The AV1, AC2, and AC3 genes showed strong purifying selection, as indicated by highly negative dN–dS values and statistically significant p-values. In contrast, AV2 and AC5 exhibited weak purifying selection, suggesting relatively relaxed evolutionary constraints on these genes. Notably, the AC4 gene displayed a positive dN–dS value, indicating evidence of positive selection, although with marginal

statistical support (Table 4). Overall, these results suggest that while the majority of begomovirus genes are conserved, certain genes such as AC4 may be undergoing adaptive evolution. Comparable findings were reported in 2019 by Mondal *et al.* [20].

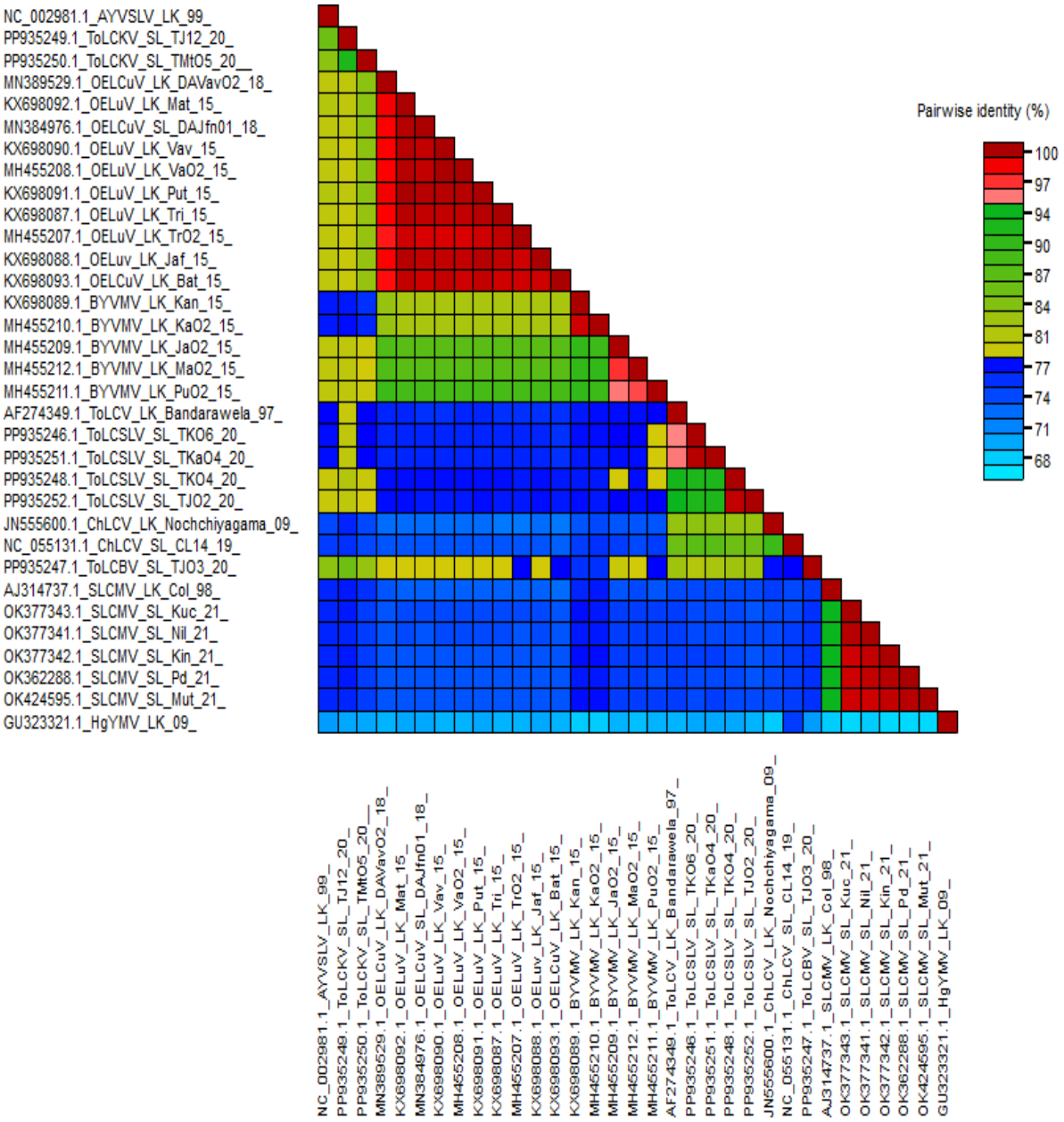

Figure 1. Pairwise identity matrix using complete nucleotide sequences of different begomovirus isolates from Sri Lanka by SDT (version 1.2).

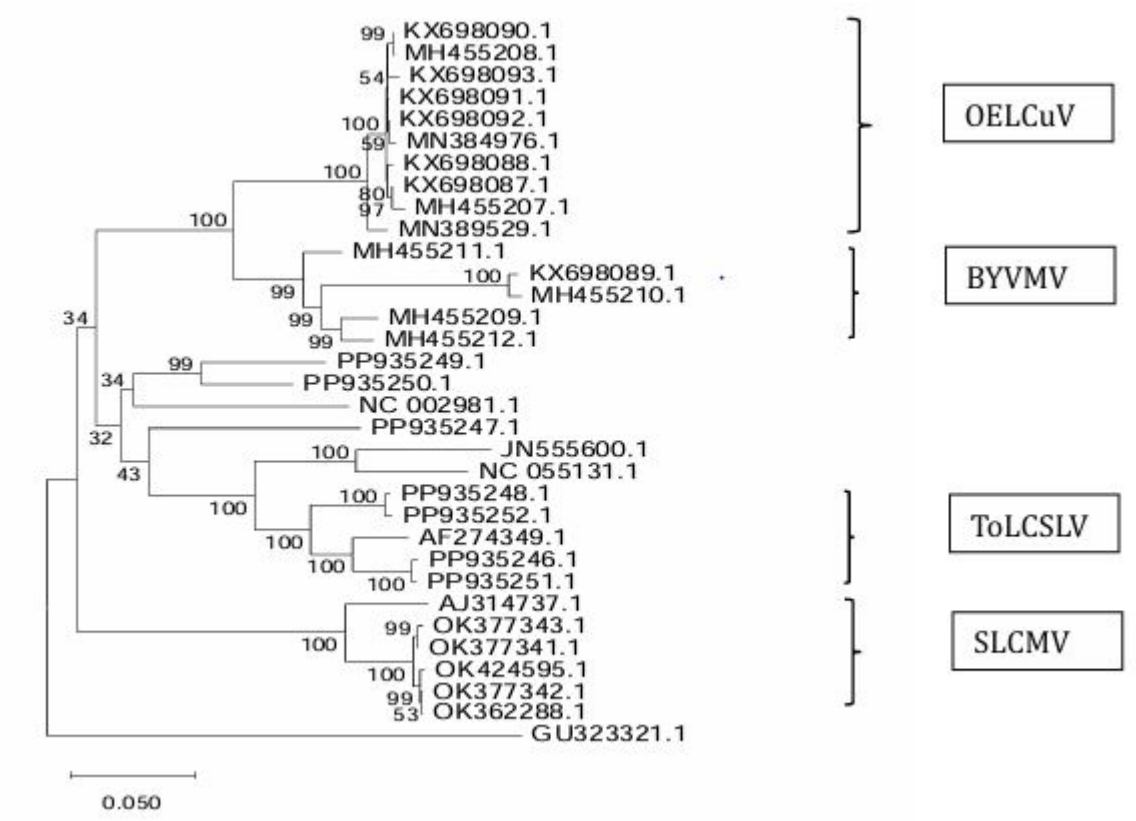

Figure 2. Phylogenetic tree of complete nucleotide sequences of begomoviruses reported from Sri Lanka. The tree was generated using Neighbor-joining method in MEGA 12. Horizontal distances are proportional to sequence distance, vertical distance is arbitrary. A bootstrap analysis with 1000 replicates was performed and the bootstrap percent values are numbered along branches.

Table 3. Recombination events detected using RDP4 (Recombination Detection Program) within begomoviruses reported from Sri Lanka, based on full-length DNA-A sequences

Event	Break point		Recombinant	Parents		Methods	p-value
	Begin	End		Major	Minor		
01	66	1996	ChLCV(SL:CL14:09)	ChLCV(LK:Noc:09)	ToLCSLV(LK:TKaO4:20)	R,G,M,C,S	1.369E-17
02	68	488	ChLCV(LK:Noc:09)	Unknown	ToLCSLV(LK:TKaO4:20)	R,M,C,S	9.745E-10
03	2692	2735	ToLCBV(SL:TJO3:20)	OELCuV(LK:TrO2:15)	SLCMV(LK:Col:98)	R,M	5.199E-07
04	2704	39	AYVSLV(LK:99)	Unknown	BYVMV(LK:JaO2:15)	R,G,B,M,C	1.417E-07
05	-	2454	ChLCV(LK:Noc:09)	ToLCSLV(LK:Ban:97)	Unknown	G,M,C	2.639E-07

Table 4. Selection pressure analysis on begomovirus gene

Gene	Probability value (p) (p<0.01)	Statistical value (dN-dS)	Selection pressure
AV1	0.00	-9.65	Strong purifying selection
AV2	0.41	-0.82	Weak purifying selection
AC2	0.00	-3.04	Strong purifying selection
AC3	0.00	-4.45	Strong purifying selection
AC4	0.05	1.99	Positive selection
AC5	0.79	0.27	Weak purifying selection

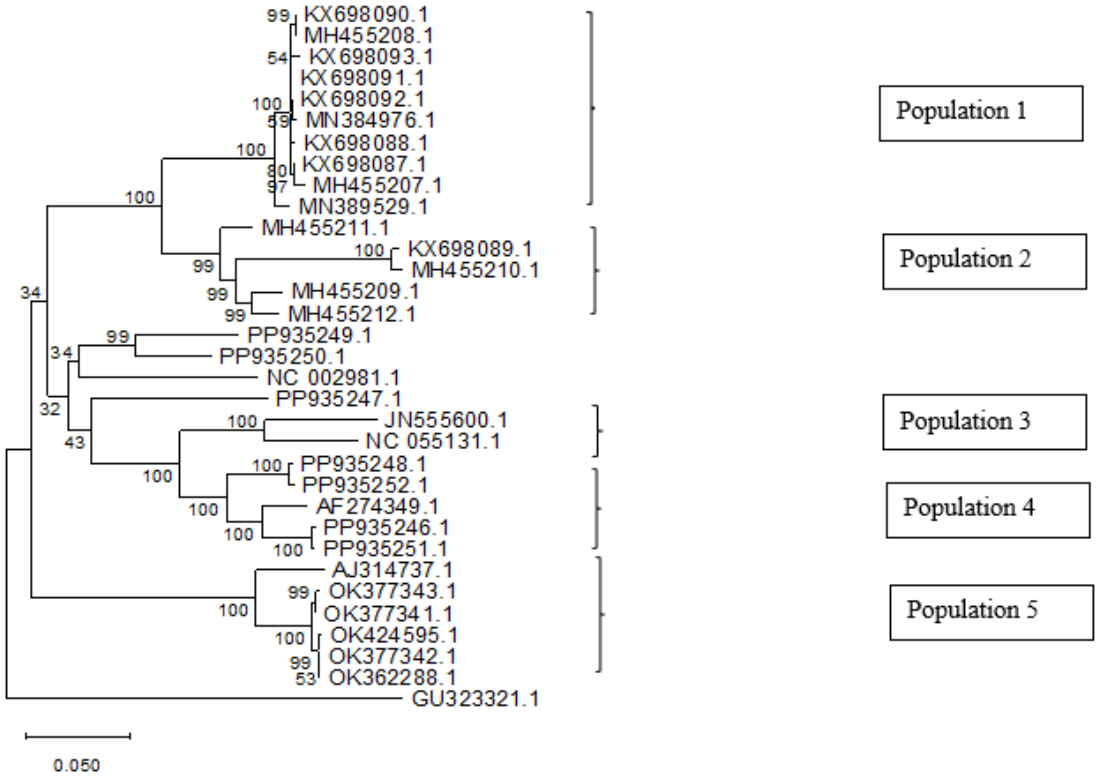

Figure 3. Nucleotide diversity analysis using complete nucleotide sequences of begomovirus.

3.6 Nucleotide diversity analysis

Population 1 comprises ten isolates of OELCuV, while population 2 includes five isolates of BYVMV, Population 3 consists of two isolates of ChLCV, whereas population 4 contains five isolates of ToLCSLV. Population 5 made up of six isolates of SLCMV (Figure 3).

The analysis of mean nucleotide diversity revealed variation among the five populations of begomoviruses in Sri Lanka (Table-5). Population 3 showed the highest nucleotide diversity (0.19), indicating greater genetic variability within this group, while Population 1 exhibited the lowest diversity (0.01), suggesting a more conserved genetic structure. Populations 2 and 4 displayed moderate and similar levels of diversity (0.08), whereas Population 5 showed relatively low diversity (0.04). The overall nucleotide diversity of the entire population was 0.20, reflecting substantial genetic variation when all populations are considered together. These results indicate uneven distribution of genetic diversity among populations, with certain groups contributing more significantly to the overall variability.

Table 5. Mean nucleotide diversity for each population and entire population

Mean nucleotide diversity	Value
Population 1	0.01
Population 2	0.08
Population 3	0.19
Population 4	0.08
Population 5	0.04
Entire population	0.2

4. CONCLUSION

Seven genetically diverse *Begomovirus* groups were reported in Sri Lanka. Such as; AYVSLV, ChLCV, HgYMV, OELCuV, BYVMV, SLCMV, and ToLCV. Phylogenetic analysis and pairwise identity matrices revealed four dominant *Begomovirus* populations in Sri Lanka: OELCuV, OYVMV, SLCMV, and ToLCSLV. The identified strains represent the most agriculturally significant populations in the region. Evidence of recombination detected in several genomes indicates ongoing evolutionary processes that may contribute to the emergence of novel strains. Furthermore, variations in nucleotide diversity among populations suggest the influence of distinct evolutionary pressures and adaptation mechanisms across different geographic and ecological settings. These findings provide valuable insights into the genetic diversity and evolutionary dynamics of the pathogen populations, with important implications for disease management and crop protection strategies.

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