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Research article

Phylogenetic and evolutionary analysis of papaya leaf curl viruses infecting a diverse host range: An *in-silico* approach

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ABSTRACT

Papaya leaf curl virus belongs to the largest family of plant viruses Geminiviridae and genus Begomovirus that causes a very devastating disease in papaya known as leaf curl disease. Curling in leaves is the most prominent and typical symptom in the host plants. Yellowing and thickness of veins are other characteristic symptoms of the disease. In recent few decades, Papaya leaf curl viruses have been noticed to infect a range of hosts other than papaya including weed and non-weed crops. Leaf curl disease causes severe symptoms in plants leading to the stunted growth and ultimately yield loss. They have been proved to be one of the most devastating biotic factors for the production of highly economical crops including papaya, chili, tomato, soybean, radish, jasmine etc. In this study, the genomic sequences of papaya leaf curl viruses isolated from different hosts were taken to assess the diversity and phylogenetic relationship among them. The isolates in the study were found to be related to same species, they were more or less closely related but evolved to infect a diverse host range. This approach can eventually lead to the development of a unified mechanism to prevent the outbreak of the leaf curl disease globally.

1. Introduction

Papaya leaf curl virus (PaLCuV) belongs to genus *Begomovirus* of *Geminiviridae* family, is primary cause of one of the most prevalent diseases of papaya which is papaya leaf curl disease and thus affecting its production worldwide (Soni et al., 2022; Srivastava et al., 2022). The host plants get infected with PaLCuV through whitefly aphid (*Bemisia tabaci*), which serve as vector for viral transmission (Varun et al., 2017). PaLCuV is a phloem-bound virus and can be transmitted mechanically. The infection was initially identified in India by Thomas and Krishnaswamy in 1939, which was later confirmed by a detailed study of the disease causative organism in 1998 by Sangeeta Saxena and colleagues (Saxena et al., 1998). Highly wrinkled and exclusive inwardly curled patterns that forms an inverted cup-shaped structure is the characteristic symptom of the plants infected with PaLCuV (Soni et al., 2022; Srivastava et al., 2022). The other symptoms include smaller leaves, vein thickening, chlorosis, mosaic pattern, yellowing of veins, twists in petioles to form zigzag pattern and

overall stunted growth of the plants. The PaLCuV infection not only affects the morphological features but also reduces the phytochemical constituents and properties in the infected plants.

1.1 Genome organization of PaLCuV

Begomoviruses are non-enveloped, circular single-stranded DNA (ssDNA) particles of approximately 2.7- 2.8 kb in size. Begomovirus are classified as either monopartite segment of DNA-A or bipartite segment of DNA-A and DNA-B (Lozano et al., 2016; Zhou, 2013). Additionally, ssDNA assistance molecule labelled as beta-satellite or alpha-satellite (Fig. 1) and a recently discovered delta-satellite are associated with monopartite viruses. The genome of the virus consists six open reading frames (ORFs) namely AV2 (pre-coat protein), AV1 (coat protein), AC3 (Replication enhancer protein), AC2 (Transcriptional activator protein- TrAP), AC1 (Replication initiation protein- Rep) and AC4 that are separated by an intergenic region (IR) and are organized into two transcriptional orientations (Nehra et al., 2019). These proteins

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help transport the viral particles both intra- and intercellular within the host. Moreover, the highly conserved and invariant nona-nucleotide sequence “TAATATTAC” along with an origin of replication, is present in this intergenic (IR) region which forms hairpin loops and play crucial role in DNA replication (via rolling circle mode) and RNA transcription in Geminivirus (Varun et al., 2017). Furthermore, the majority of monopartite viruses are linked to beta-satellite, which encodes a significant β C1 protein at complementary sense strand and is involved in disease epidemics, transcriptional and post-transcriptional gene silencing and induction of infection symptoms (Varun et al., 2017; Zhou, 2013).

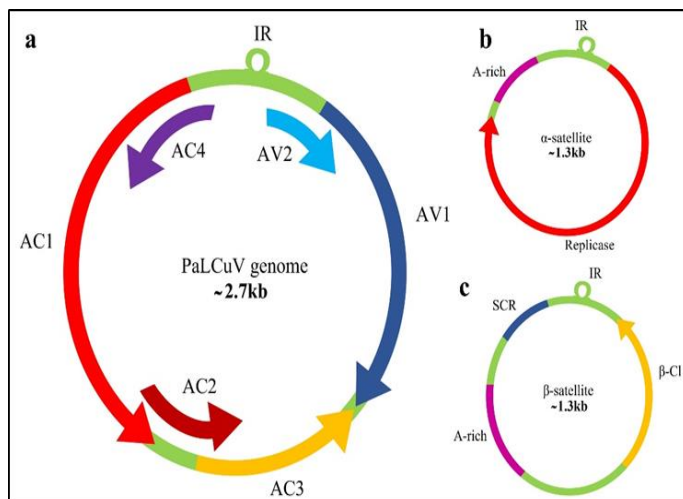


Fig. 1 Genome organization of PaLCuV a DNA-A b α -satellite c β -satellite

1.2 Host range of PaLCuV

As far as the host range is concerned, leaf curl viruses have been revealed with an extensive host range in both weed and non-weed crops (Varun et al., 2017). Ageratum, Malvastrum and Croton are some examples among weed species that are evident host for this virus (Hallan et al., 1998). Apparently, weeds are considered as the viral reservoir, which are known to spread the infection during the non-cropping seasons thereby acts as substitute source of Geminivirus (Varun et al., 2017). PCR based diagnostics and molecular detections have revealed their extensive manifestation within themselves or in association with non-weed crops as hosts. For instance, *Corchoropsis timentosa* is a weed and was found as an alternative host for papaya leaf curl China virus as the AV2 gene of infected weed showed 98.9% sequence similarity (Huang and Zhou, 2006). Similarly, the radish leaf curl virus was reported to be present in chili plant which was identified by coat protein gene similarity from phylogenetic relationship analysis. Besides, the occurrence of papaya leaf curl China virus infection was also found in *Sigesbeckia orientalis*, a weed species in China as first report along with *Sigesbeckia* yellow vein virus and its β -satellite (Yang et al., 2011). Among the non-weed crop hosts for PaLCuV, the molecular interventions made it possible to assess the infection of papaya leaf curl virus in tobacco plant in India, which was further co-detected in tomato leaf curl New Delhi virus using PCR-based findings. (Raj et al., 2008). The fact of Geminivirus having a multiple

host range is becoming highly evident due to which the infection regulatory measures are getting more challenging and is yet an avenue to be explored with prospective research. As per the study, papaya leaf curl China virus was identified from tomato plant with leaf curl symptoms and further investigated the infection by Agro-inoculating the constructed clone of papaya leaf curl China virus (PaLCuCNV) in *Nicotiana tabacum*, *Nicotiana benthamiana*, *Nicotiana glutinosa*, *Petunia* and *S. lycopersicum* (Zhang et al., 2010). The Agro-infected plants eventually developed the distinct symptoms of severe curling which was further confirmed by southern blotting and PCR based diagnostics thereby, concluded these plant species as potential hosts for PaLCuCNV (Zhang et al., 2010). Present study is mainly emphasizing on the diversity and relatedness among PaLCuV isolates infecting a range of host other than papaya. The evolutionary patterns among the isolates were also analyzed by phylogenetic studies.

2 Materials and methods

All the data used in this study was obtained from National Center for Biotechnology Information (NCBI, <https://www.ncbi.nlm.nih.gov/>). For the proposed study, whole genome sequences of PaLCuV were downloaded in FASTA format. A total of 23 sequences were found from PaLCuV isolates infecting different hosts including papaya. The accession numbers of all the representative isolates were as follows MW816852.1, MN839534.1, MK087120.1, JQ954859.1, JN135233.1, HM143914.1, OR489166.1, OL542831.1, MF278787.1, KY926899.1, KX353619.1, JN817517.1, FJ593629.1, DQ629102.1, KY978407.1, KT253647.1, KC161184.1, AJ436992.1, JN807765.2, LN878129.1, LN845920.1, FM955601.1 and JN703795.1 which are given in Table 1. Additional information regarding the sequences and their respective hosts from where they have been isolated and the symptoms they caused in them are also given in Table 1.

2.1 Pairwise sequence comparison (PASC) among the sequences

PASC is a genome-based tool that was used to classify and identify the isolate diversity for being either within species, genera or family. <http://www.ncbi.nlm.nih.gov/sutils/pasc/> is provided to go through the PASC datasets which stores complete genome data of around 56 virus families. PASC was done within the Geminiviridae family to classify the sequences retrieved.

2.2 Multiple sequence alignment and phylogenetic analysis

Multiple sequence alignment (MSA) of the retrieved sequences was done by using MEGA11 software (Tamura et al., 2021). MSA was done to find out the similarity among the genomes of PaLCuV isolates infecting a range of hosts and to proceed for phylogenetic analysis. Phylogenetic analysis was done to find out the evolutionary mechanism and relatedness among the selected PaLCuV isolates. For phylogenetic analysis MEGA11 software was used. The evolutionary tree was inferred by using Neighbor-joining program enabling bootstrap method with 1000 replicates.

Table 1 Isolates of PaLCuV infecting various hosts as given in column three and their respective accession numbers and genome length given in column four and column five, respectively

S. No.	Isolated from host	Accession no.	Genome size (in bp)	Symptoms identified
1.	<i>Crotalaria juncea</i> (Indian hemp)	MW816852.1	2758	Curling of leaves (Venkataravanappa et al., 2022)
2.	<i>Cestrum nocturnum</i> (night jasmine)	MN839534.1	2737	Curling and rolling of leaves (Lal et al., 2020)
3.	<i>Calendula</i> (marigold)	MK087120.1	2773	Curling and yellow vein in leaves
4.	<i>Aster alpinus</i> L. (alpine aster/blue daisy)	JQ954859.1	2746	Yellow vein (Srivastava et al., 2013)
5.	<i>Amaranthus cruentus</i> L. (red amaranth)	JN135233.1	2746	Curling of leaves and stunted growth (Srivastava et al., 2015)
6.	<i>Nicotiana glutinosa</i> (Peruvian tobacco)	HM143914.1	2746	Curling and yellow vein in leaves
7.	<i>Carica papaya</i> (papaya)	OR489166.1	2758	Curling of leaves
8.	<i>Dioscorea</i> (yam)	OL542831.1	2746	Curling of leaves
9.	<i>Codiaeum variegatum</i> (garden croton)	MF278787.1	2758	Curling of leaves and vein thickness (Akram et al., 2020)
10.	<i>Populus alba</i> (white poplar)	KY926899.1	2756	Curling of leaves
11.	<i>Catharanthus roseus</i> (sadabahar)	KX353619.1	2756	Leaf yellowing and curling (Marwal et al., 2021)
12.	<i>Croton bonplandianus</i> (ban tulsi)	JN817517.1	2745	Yellow vein mosaic (https://doi.org/10.21203/rs.3.rs-3420362/v1)
13.	<i>Raphanus satyvus</i> (radish)	FJ593629.1	2759	Curling of leaves (Singh et al., 2007)
14.	<i>Solanum sp.</i> (cherry tomato)	DQ629102.1	2751	Curling and distortion of leaves and stunted growth of plant (Pandey et al., 2010)
15.	<i>Capsicum sp.</i> (Chili)	KY978407.1	2741	Curling of leaves
16.	<i>Cyamopsis tetragonoloba</i> (cluster bean)	KT253647.1	2756	Curling of leaves
17.	<i>Passiflora edulis</i> (passion fruit)	KC161184.1	2732	Leaf mottling and malformation (https://doi.org/10.1094/PDIS-05-13-0554-PDN)
18.	<i>Gossypium sp.</i> (cotton)	AJ436992.1	2753	Curling of leaves, vein thickness and darkening (Mansoor et al., 2003)
19.	<i>Glycine max</i> (soybean)	JN807765.2	2746	Yellow vein mosaic
20.	<i>Solanum lycopersicum</i> (tomato)	LN878129.1	2750	Curling of leaves
21.	<i>Physalis peruviana</i> (rasbhari)	LN845920.1	2752	Curling of leaves, vein thickness and chlorosis (Tahir et al., 2017)
22.	<i>Rhynchosia capitata</i> (clustered-flower snoutbean)	FM955601.1	2754	Yellow mosaic (Ilyas et al., 2010)
23.	<i>Euphorbia pulcherrima</i> (flame leaf)	JN703795.1	2736	Curling of leaves

3. Results and discussion

3.1 Pairwise sequence comparison (PASC)

Geminiviridae is the largest known family of viruses till date which comprises nine genera based on host specificity, genome organization and their vector (Hanley-Bowdoin et al., 2000). The nine genera of the family are *Becurtovirus*, *Capulovirus*, *Eragrovirus*, *Begomovirus*, *Curtovirus*, *Topocuvirus*, *Mastrevirus*, *Turncurtovirus* and *Grablovirus* (Varsani et al., 2017). PASC was done to identify the isolates belonging to

either same species, genus or family. The maximum similarity percentage was found between MN839534.1 and KY978407.1 (96.82%); whereas, the minimum percentage similarity was found between JN817517.1 and JN703795.1 (68.38%). PASC eventually indicated that all the selected isolates belonged to same species (Fig. 2). The highest similarity percentage between any two of all the retrieved sequences is given in the Table 2.

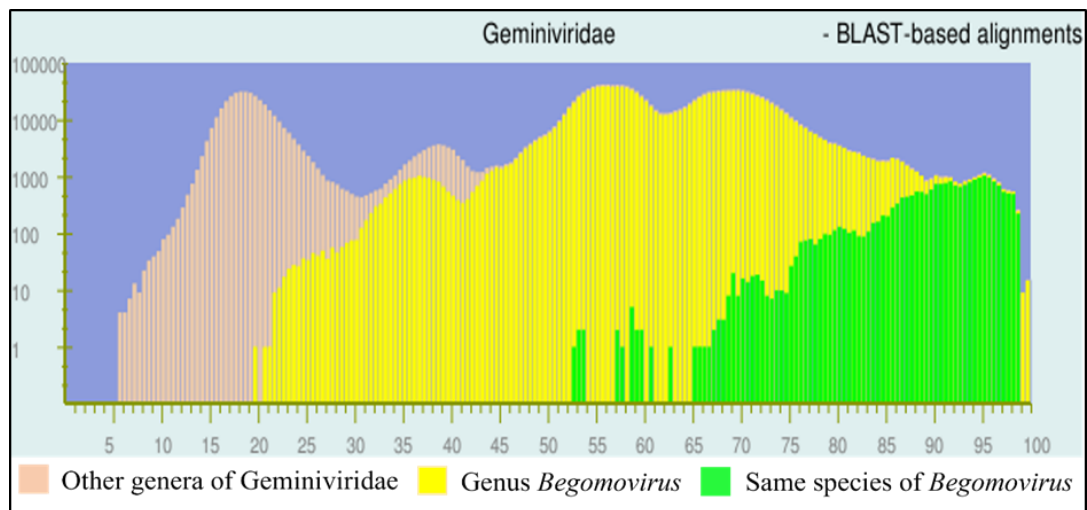


Fig. 2 Pairwise sequences comparison (PASC) of PaLCuV isolates, the yellow-, green- and peach-colored parts of the graph are representing the genus *Begomovirus*, same species of genus *Begomovirus* and other genera of family *Geminiviridae*, respectively

Additionally, MW816852.1, MK087120.1, KC161184.1 were showing 94.07, 93.19 and 92.16 % of sequence similarity with radish leaf curl virus (GU732204.1), Croton yellow vein mosaic virus (JN817516.1), papaya leaf curl Guangdong virus respectively. JN135233.1, HM143914.1, OL542831.1 and JN807765.2 were showing 94.39, 94.79, 93.01 and 93.66% of sequence similarity respectively with papaya leaf curl virus (Y15934.1).

3.2 Phylogenetic analysis

Evolution and advent of novel *Begomovirus* species involves recombination and mutation events (Silva et al., 2014). Full-length genomic sequences of 23 PaLCuV isolates were used to assess the phylogenetic relationship among them. Since it is well known that PaLCuV belongs to genus *Begomovirus* and is having quite dissimilarity with other viruses causing diseases in papaya. However, PaLCuV itself consist of a diverse genetic variation and that's why this phylogenetic study was done to find out the relationship among PaLCuV isolates which were infecting different hosts. For the proposed study, the whole genome sequences of PaLCuV isolates were retrieved from GenBank. The phylogenetic study was carried out by MEGA11 using Neighbour-joining algorithm and bootstrap method with 1000 replicates for the MEGA aligned sequences. Genome sequence of papaya leaf curl virus Delhi isolate (OR489166.1) was taken as an out group. Neighbour-joining tree prepared after a resolution of 1000 replicates is shown in Fig. 3. The tree was unrooted indicating towards uncommon ancestors and revealed that all the PaLCuV isolates were grouped into one large and one small cluster. The smaller cluster was found very distinct from the larger one and consisted of PaLCuV isolates found in Taiwan infecting *Passiflora edulis* (KC161184.1) and *Euphorbia pulcherrima* (JN703795.1) which were sharing high similarity between them with 100 bootstrap frequency. The rest of the PaLCuV genomes were from India and Pakistan forming the larger cluster. The larger cluster was further divided into four subclusters. OL542831.1, JQ954859.1, JN135233.1, HM143914.1, JN807765.2 were lying in the same clade and probably having the common ancestors. MW816852.1

(PaLCuV isolate on *Gossypium*, India) and AJ436992.1 (PaLCuV isolate on *Crotalaria juncea*, Pakistan) were sharing 91.78% of sequence homology and were very closely related to each other in the phylogenetic tree.

LN878129.1 PaLCuV isolate on *Solanum lycopersicum*, Pakistan) and KY978407.1 (PaLCuV isolate on *Capsicum*, Pakistan) both were lying in different clades but were very closely related. Due to natural as well as trade barriers the PaLCuV isolates from India and Pakistan were dominating particular portions of the phylogenetic tree although with some exceptions. The results obtained from PASC and phylogenetic analysis shows that although the isolates belonged to the same species but probably they are evolved from uncommon ancestors. Furthermore, in vivo and in vitro studies can contribute in the development of a common strategy to prevent the leaf curl disease on various hosts.

4. Conclusion

The study finds high sequence similarity among the sequences obtained from different hosts. High similarity percentage indicated that the isolates were falling into a narrow taxonomic criterion probably belonging to same species as per the results of PASC. The phylogenetic tree was however unrooted which means they are not evolved from common ancestors and this might the probable reason of their diverse host range. The results of phylogenetic analysis showed that the species were falling in the same clade were somehow specific to a particular geographical location with a few exceptions which indicated that the emergence of those species followed different evolutionary patterns but eventually they shared higher sequence homology which showed that they might have gone through the process of convergent evolution. Different geographical regions that are separated by natural barriers or separated through allopatric speciation may lead to the evolution of new species of viruses capable of affecting various other hosts too. Further, detailed in vivo genomic studies and molecular characterization of the isolates infecting a vast range of host crops can lead to the development of a unified

preventive mechanism to stop the outbreak of this severe disease.

Table 2 Representing percentage similarity among the sequences retrieved (local matches) and other top matches

S. No.	Top matches among retrieved sequences			Other top matches (other than the retrieved ones)
	Query sequences	Local matches	Percent match	
1.	MW816852.1	AJ436992.1	91.78%	MW816852.1 with GU732204.1 (94.07%)
2.	MN839534.1	KY978407.1	96.82%	-
3.	MK087120.1	FJ593629.1	91.07%	MK087120.1 with JN817516.1 (93.19%)
4.	JQ954859.1	JN135233.1	91.51%	-
5.	JN135233.1	HM143914.1	93.12%	JN135233.1 with Y15934.1 (94.39%), HM143914.1 with Y15934.1 (94.79%)
6.	OR489166.1	MN839534.1	94.55%	-
7.	OL542831.1	HM143914.1	92.17%	OL542831.1 with Y15934.1 (93.01%)
8.	MF278787.1	FM955601.1	92.08%	-
9.	KY926899.1	KT253647.1	96.41%	-
10.	KX353619.1	DQ629102.1	93.58%	-
11.	JN817517.1	FJ593629.1	93.45%	JN817517.1 with AJ507777.1 (95.63%), FJ593629.1 with JN663850.1 (99.76%)
12.	KC161184.1	JN703795.1	91.77%	KC161184.1 with FJ869907.1 (92.16%), JN703795.1 with FJ869907.1 (98.7%)
13.	AJ436992.1	LN845920.1	94.49%	AJ436992.1 with GQ200446.1 (95.46%)
14.	JN807765.2	HM143914.1	90.82%	JN807765.2 with Y15934.1 (93.66%)
15.	LN878129.1	KY978407.1	92.62%	-
16.	FM955601.1	AJ436992.1	93.91%	-

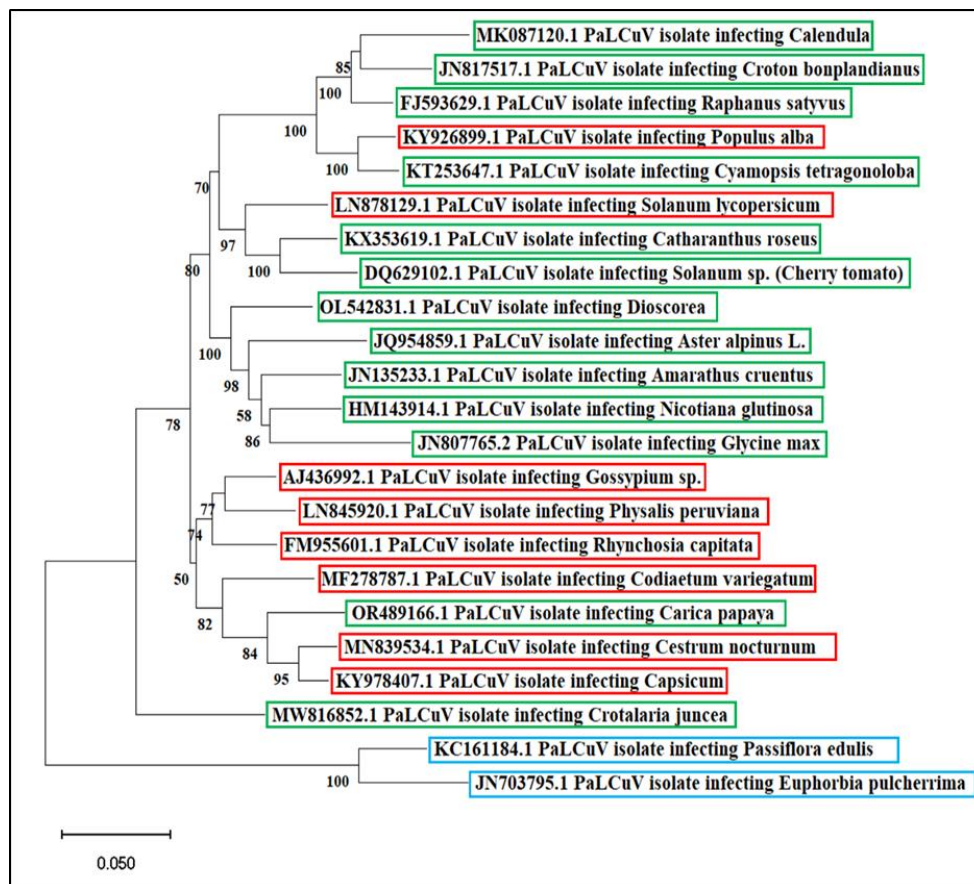


Fig 3. Phylogenetic tree of PaLCuV isolates from various hosts prepared from neighbor-joining algorithm employing bootstrap method with 1000 replicates. Indian and Pakistani isolates are highlighted with green and red colors respectively whereas the isolates from Taiwan are highlighted with blue color

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Declaration of Conflict of Interest

The authors do not have any competing interest to declare and is relevant to the content of this article.

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