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Expanding Host Range of Papaya Leaf Curl Virus (PLCV) into Agricultural Crops and Weeds Species

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ABSTRACT: The papaya leaf curl virus (PLCV) (genus Begomovirus, family Geminiviridae) poses a major constraint to papaya production, as it causes one of the most predominant and economically important disease affecting papaya in the Indian sub-continent. The virus has been fast extending its host range worldwide. In the last decade, extensive research on the genome sequence, structure and function, encoded protein functions, recombinant studies, and plant–virus interactions have been conducted. Special emphasis has been given to genome structure, genetic variability, and recombination studies as well as on plant defense strategies. These studies have provided new insights in the host range, host adaptation, and evolution of the virus and the structural differences between the new and the old-world complexes. Understanding the rapid expansion of plant viruses in general and begomoviruses in particular is a major challenge that needs to be studied in greater details to devise measures for crop protection in future to come. It has been established that plant viruses are spreading at an alarming rate as suggested by the rapid genome evolution and high dN/dS rates (nucleotide substitution rate). This paper highlights the host expansion of PLCV over a period of two decades (2000 to 2020) where PLCV has shown tendency to evolve from a host specific virus to a more generalist begomovirus infecting a range of hosts that are of agricultural and/or horticultural importance and a number of weed species. The full-length genomic sequence of begomoviral PLCV isolates from non-papaya hosts are analyzed using MEGA 11.0. From the molecular phylogenetic analyses and percent identity matrix, it is shown that there is a clear sub-division of these begomoviral PLCV infecting non-papaya host species into an Indian group consisting of sequences from India as well as Pakistan and on the other hand, the China Group consisting of sequences reported from China, Taiwan and Vietnam. The distribution of these begomoviral isolates used in this study showed a clear discernable pattern based on geographical proximity. Thus, the present work indicates evolution of PLCV strains infecting a number of angiosperm families into two major groups based on their nucleotide sequence similarity.

Keywords: Papaya Leaf Curl Virus (PLCV), Begomovirus, Geminiviridae, Host expansion.

INTRODUCTION

Geographical Distribution, Host Range and Epidemics. Since the time when the first virus disease in papaya was described in 1929 from Jamaica (Smith, 1929), a number of diseases in papaya caused by different groups of plant viruses have been reported from papaya-producing areas in the world as a major limiting factor for papaya cultivation and papaya production (Adsuar, 1946; Capoor and Verma, 1948; Harkness, 1960; Lastra and Quintero, 1981; Wan and Conover, 1983; Chandra and Samuel, 1999). Among the different viruses infecting papaya, papaya ring spot diseases caused by Papaya Ring Spot Virus (PRSV) of family Potyviridae and papaya leaf curl disease caused by Papaya Leaf Curl Virus (PLCV) of family Geminiviridae cause major threat for papaya production in India and other papaya growing countries (Chitra *et al.*, 2019; Reena *et al.*, 2022).

Out of PRSV and PLCV, latter is an important constraint to papaya production in particular, as it causes one of the most predominant and economically important diseases affecting several varieties of papaya in the Indian subcontinent. Papaya leaf curl disease was reported for the first time in India in 1939 by Thomas from Madras. The virus causes devastating disease of papaya characterized by upward or downward leaf curling, leaf crinkling and crumpling of leaves, vein clearing and thickening, yellow mottling, leaf puckering, blistering of leaves and general deformation of leaves. In the later stages of the infection, plants appear stunted with shortened internodes and show impaired fruit setting, leading to complete crop loss (Singh-Pant *et al*., 2012). In recent years, incidence and severity of leaf curl disease is increasing in papaya fields in India (Nariani, 1956; Saxena *et al.,* 1998a-c) resulting in severe economic losses.

In recent years, incidence of PLCV infection has been reported from different regions of the world in papaya as well as in a number of species of agricultural, horticultural importance and in a number of weed species too. Table 1 shows the countries from where the PLCV has been reported till date.Earlier epidemics of PLCV were reported from Asian and African Countries with majority reports coming from India, Pakistan, China, Bangladesh, Thailand, Sudan, Egypt, and some other countries.

The papaya leaf curl virus (PLCV) is a monopartite begomovirus species belonging to Genus Begomovirus, Family Geminiviridae and is transmitted by white fly *Bemisia tabaci* (Gennadius) as the vector for virus transmission (Nariani, 1956). It has a circular, single stranded DNA (2.7Kbapprox.) called DNA-A (Saxena *et al.,* 1998b). The PLCV genome is occasionally found to be associated with smaller DNA molecule called Alpha and Beta Satellites of 1.3Kb size approximately (Saxena *et al*., 1998a-c).

PLCV has been recently reported to diversify its host range from Papaya to seasonal vegetable crops and other fibre crops (Varun and Saxena 2018). Generally, the Gemini viruses associate with a specific host for its multiplication and hence, infection. However, the host specificity is now being reported by many workers to be evolving into host non-specificity or a broader range of host specificity indicating expanding viral genome base over time. Such a host range expansion indicates evolution in the viral genome to diversify and thus establish infection into other crops which were earlier considered begomoviral non-host species. The situation has been rapidly changing as the virus is now fast spreading to larger stretch of these geographical regions and expanding its host range. The virus has an extensive host range now and is found in a number of host plants including many weeds. The virus infects *Nicotiana tabacum* (tobacco), *Lycopersicon esculentum* (tomato), *Crotalaria juncea* (sun hemp), *Capsicum spp.* (Chilli), *Petunia*, *Zinnia*, and *Daturastramonium*, *Ageratum*, Cucurbits, Soybean (Jaidi *et al.,* 2015); *Jatropa* (More *et al*., 2019) and other vegetable crops.

The host range extension also indicates virus selecting for alternate hosts as a survival mechanism. Further, switching of the PLCV between perennial host (such as papaya) to seasonal host (such as agricultural crops) has enabled the virus to be a bigger threat to the crop growers and to the crop yield over time. Also, viral infection and viral load in weeds or in agricultural or horticultural crops may play a possible role as a reservoir host in transmission of this virus. The expansion of the virus is thus becoming rapid and effective over time and space. The present paper discusses the expanding host range of PLCV over the last two decades into non-papaya host species and tries to discern underlying patterns of their rapid host expansion in the last two decades.

MATERIALS AND METHODS

Begomoviral PLCV isolates (full length and betasatellites) reported from non-papaya host were obtained from NCBI GenBank Database. NCBI website was accessed between 01.06.2021 to 25.10.2021. Full-length DNA-A genomic component sequences and Beta-satellite sequences are available for isolates of PLCV infection reported from different cultivated plant species as well as weeds. Table 2 summarizes the various full length begomoviral PLCV isolates reported from host species other than Papaya. Table 3 summarizes the PLCV Betasatellites isolates reported from non-papaya host species.

Nucleotide sequence used in the study. A total of 109 full length begomoviral PLCV isolates were obtained from NCBI GenBank (www.ncbi.nlm.nih.gov/nucleotide). Out of these 109, only 09 sequences belonged to PLCV reported from Papaya from different regions. These09PLCV isolates from papaya were randomly selected as reference sequence for the purpose of standard referencing and comparison based on sequence similarity. Remaining 100 sequences are full length begomoviral PLCV isolates reported from non-papaya host species as mentioned in Table 2. The accession number and the species from where these are reported is mentioned in Table 2. These 109 sequences were subjected to same treatment and were used in all downstream analyses.

Percent Identity Matrix(PIM) Analyses. The 109 full length begomoviral PLCV sequences were subjected to percent identity matrix analyses using Mega 11.0 version (available at www.megasoftware.net; Tamura *et al*., 2021). The percentage identity so obtained was manually color coded using the scheme: Green color for all the pairs with 97% and above identity, Yellow color for all the pairs with 96.99%-90% identity, Blue color for 89.99%-.80% and Red color for all the pairs for 79.99% and less.

Multiple Sequence Alignment. The entire dataset of 109 full length begomoviral PLCV sequences as mentioned earlier were converted to FASTA format and subjected to multiple sequence alignment (MSA) using Clustal W package (Thompson *et al.,* 1994) built in the MEGA 11.0 software (Tamura *et al.,* 2021). The sequences were truncated at the start of the sequences for making an equal length alignment with a total of 2937 positions (including gaps).

Phylogenetic Tree Construction. The multiple sequence alignment file was subjected to phylogenetic and molecular evolutionary analyses using MEGA version 11 (Tamura *et al.,* 2021). The parameters deployed in phylogenetic analyses were: Statistical method: (ML) Maximum Likelihood; Test of Phylogeny: Bootstrap Method; No. of Bootstrap Replications: 1000; Substitutions Type: Nucleotides, Model/Method: Tamura-Nei Method; Rates among sites: Gamma Distributes with invariant sites (G+I); No. of discreet gamma categories: 5; Gap/missing data treatment: use all sites; Select codon positions: Tick all; ML Heuristic method: Nearest-Neighbour Exchange (NNI); Initial Tree for ML: Make initial tree automatically; Branch Swap Filter: None; Number of threads: 3. It took nearly 38 hours to complete the phylogenetic tree construction. The ML tree thus obtained was saved in PNG format for further analyses.

RESULTS AND DISCUSSIONS

Begomoviral PLCV reported from non-papaya host species. Table 2 depicts the begomoviral PLCV sequences reported in the NCBI GenBank database that have been found to cause leaf curl disease of plant species other than papaya.

PLCV, like most monopartite begomoviruses is involved in the major disease complexes affecting various crops in the "Old World" causing diseases in a number of plants belonging to (but not limited to) families including *Asteraceae, Amaranthaceae, Apocynaceae, Solanaceae, Euphorbiaceae, Fabaceae, Gentianaceae, Malvaceae, Passifloraceae, Saliacaceae, Acanthaceae, Brassicaceae*. The effects are economically most devastating in Solanaceae. PLCV complex initially reported in Papaya crops is now affecting vegetable and other crops along with a number of weeds. It has been documented that PLCV infects 29 different plant species as reported in Table 2. These reports of PLCV infecting non-papaya species has been reported from Bangladesh, China, India, Indonesia, Iran, Italy, Malaysia, Pakistan, Sri Lanka, Spain, Taiwan, Thailand, Tunisia & Vietnam. Table 3 summarizes Betasatellites associated with PLCV reported from non-papaya host species. These species from where DNA Betasatellites have been reported belong to agriculturally important species such as grain legumes (*Vigna radiata)*,Tomato, and some weed species such as *Parthenium hysterophorus* (Kumar *et al.,* 2016) and *Pseuderanthemum reticulatum.*

In 2003, the association of PLCV with leaf curl disease on non-papaya host was reported for the first timeby Mansoor *et al.* (2003a-b). Subsequently, over the period 2003-2020, PLCV was identified in 29 different species belonging to 12 angiosperm families. Out of these, most reports belong to *Ageratum conyzoides* (Asteraceae), *Capsicum annuum* (Bell pepper) (Kim *et al.,* 2018), *Lycopersicon esculentum* (Solanaceae), *Nicotiana* sp., (Solanaceae). These reports are mainly from India, China and Pakistan. Meanwhile, this virus has spread to various parts of the Indian sub-continent, expanding its host range drastically. Between 2000 and 2020, besides tomato, PLCV has been reported to be associated to infections of various hosts such as *Amaranthus cruentus*, *Calendula officinalis*, *Calotropis procera*, *Capsicum* sp., *Catharanthus roseus*, *Codiaeum variegatum*, *Corchoropsis timentosa*, *Crotalaria juncea*, *Croton bonplandianum*, *Cyamopsis tetragonoloba*, *Eclipta prostrata*, *Euphorbia pulcherrima*, *Eustoma grandiflorum*, *Capsicum annuum* (Bell pepper), *Glycine max*, *Gossypium* sp., *Vigna radiata*, *Kalimeris indica*, *Nicotiana glutinosa*, *Nicotiana tabacum*, *Parthenium hysterophorus*, *Passiflora* sp., *Physalis peruviana*, *Populus alba*, *Pseuderantheum reticulatum*, *Raphanus sativus* and *Rhynchosia capitata* (Table 2).

This expansion of the PLCV into a number of plant families affecting so many species of economic importance is alarming. Over two decades, this virus in particular has managed to infect such a range of species belonging to 12 angiosperm families suggest higher rates of recombinations and massive spread of the virulent strain by the vector *Bemisia tabaci*. The virus in itself can now be considered a broad-spectrum generalist as it is now found in large phytogeographical region infecting so many host species that it seems tolose its host specificity. Such a huge expansion can also indicate that the begomoviral complex may become more detrimental to the original host Papaya which is under threat due to a number of viral diseases apart from PLCV.

Percent Identity Matrix Analyses of the Begomoviral PLCV reported from non-papaya host species along with selected begomoviral PLCV reported from papaya. S1 (supplementary table) shows the percent identity matrix of the 109 full length begomoviral PLCV sequences reported from non-papaya host species as well as from papaya. As mentioned earlier, the percentage identity so obtained was color coded as per the following scheme: green color for all the pairs with 97% and above identity, Yellow color for all the pairs with 96.99%-90% identity, Blue color for 89.99%-.80% and Red color for all the pairs for 79.99% and less. Accordingly, a general study of S1indicates that the entire dataset of the sequences can be divided into following 02 sub-groups: a.) China Group that contains sequences reported from China, Vietnam, and Taiwan (Sr. No. 1-54) of S1and b.) Indian Groupthat contains sequences reported from India and Pakistan (Sr. No. 55-109) of S1.

Within the China group (Sr. 1-55), majority of the pair-wise percent sequence identity lies in the yellow coded regionindicating that most sequences within the China group have percentage identity of 90% to 96.99%. It is worth mentioning that within the China group, the sequences have been reported from a number of different non-papaya host species such as *Tomato, Ageratum, Eclipta, Tobacco, Passiflora, Corchoropsis,* *Euphorbia* which are having a sequence identity lying in yellow color-coded region *i.e.,* 96.99%-90% identity. This is followed by Red color coded region *i.e.* an identity percent of 79.99% and less. These values clearly indicate sequence divergence to a large extent within the China group indicating multiple parental types of PLCV strains from where they have spread into multiple host species.

Interestingly, within the Indian group, majority of the pair-wise percent sequence identity lies in the redcolor-coded region *i.e.* percentage identity of 79.99% or less. This is followed by second largest set of pair wise similarity lying in the blue color-coded region i.e. percentage identity in the range of 80-89.99% (S1). This result indicates very high divergence mainly due to higher frequency of recombination between very different parental types of PLCV strains that have resulted in a such a lower range of percentage identity within the Indian group (Sr. No. 55 onwards) of S1. It further indicates that not only the Indian group is slightly more divergent in its sequence composition within, but it is also more divergent than the China group, as the latter has most pairwise identity lying in yellow followed by red region. Also, within the Indian Group, the non-papaya host species reported are way more than the China Group with Tomato, Jatropha, Calendula, Croton, Radish, Cluster bean, Populus, Codiaeum, Crotalaria, Rhynchosia, Cotton, Physalis, Cestrum, Capsicum, Catharanthus, Soybean, Cape Gooseberry, Aster, Amaranthus as the major host species reported from India and Pakistan. This trend indicates geographical distribution as one of the factors behind such a stratification of the entire dataset into China and Indian group, with China, Vietnam and Taiwan grouping together and India and Pakistan grouping as one in the pairwise sequence identity matrix analysis. Further, the occurrence of lower percentage identity is suggestive of higher recombination rates and multiple parental types being responsible for the outbreak into non-papaya host species.

Multiple Sequence Alignment of the Begomoviral PLCV reported from non-papaya host species and papaya. Multiple Sequence Alignment of approx. 2736 bp long nearly full length 109 begomoviral PLCV (data not shown) revealed multiple conserved sites ranging from 10-20 bases at different intervals flanked by hypervariable regions. These highly conserved regions belong to Coat Protein (CP) or the AV1 genes and other highly conserved Inter-genic Regions (IR)/ Common Regions (CR), containing repeat sequences or Iterons and conserved putative regulatory TATA boxes regions as has been reported by other workers (Singh-Pant *et al.,* 2012; Stanley, 1995; Hanley-Bowdoin *et al*., 1999).

Phylogenetic analyses of the full length Begomoviral PLCV sequences used in this study. Fig. 1 is the Maximum Likelihood (ML) based phylogenetic tree obtained from MEGA 11.0 (Tamura *et al.,* 2021). In the phylogenetic tree so obtained, in a similar fashion as was indicated in the percent identity matrix (S1), here also the entire dataset could be sub-grouped into two major clusters i.e.the sequences reported from China, Vietnam and Taiwan hereinafter referred to as China Group and sequences reported from India and Pakistan hereinafter referred to as the Indian Group of begomoviral PLCV. The tree indicated a similar trend of sequences from different host species reported from China, Vietnam and Taiwan grouping together in multiple clusters with branches and sub-branches. Interestingly, in majority of the cases although with some exceptions, all begomoviral PLCV sequences reported from a single (non-papaya) host species were together suggesting common lineage or proximity with each other in space and time during vector mediated transmission occurring between different host species present proximally resulting in such trends. Similarly, all the sequences reported from different host species (excluding papaya ones) from India and Pakistan clustered together in a similar fashion, where in majority of cases, sequences from same species were clustered together but in some cases sequences from different species also shared the same node suggesting close relationship mainly due to direct vector transmission of the PLCV strain between the different host species. A novel strain PLCrV clustered together in the middle of the tree with no sub-branching with any other PLCV and shared the common node with the Indian group of sequences. This indicates that PLCrV is highly distinct from the rest of the begomoviral sequences. Within the Indian group, two distinct clusters can be observed, one containing majority of sequences reported from different host species in India and the other consisting of sequences reported from multiple different host species reported from Pakistan. Although in both these distinct group within the Indian group, cross-contamination of either of the two sub-groups is commonly seen. Yet, it is conclusive evidence of certain sequences being phylogenetically and molecularly more similar or parallelly evolved than the China group.

Recombination in begomoviruses as a cause and effect of host expansion. In Geminiviruses, genomic diversification and evolution has been driven by recombination events. Such phenomenon results in emergence of new recombinant viral strains. With recombinant strains comes greater biological fitness in view of higher degree of virulence as compared to their parental types from where they have been derived. Such recombinant viral strains naturally outcompete the host plant resistance strategies (Monci *et al.,* 2002). Natural genetic recombination events are common in geminiviruses, and these occur among strains, species and even within and across genera although rarely (Bisaro, 1996; Padidam *et al.,* 1999). It has also been reported that in many cases, geminiviruses occur as mixed infections with two or more virusesleading to increased viral DNA accumulation and increased symptom severity (Harrison and Robinson, 1999).

Vector mediated transmission mainly by Whitefly is another factor contributing to recombination and its increasing host range on which it can feed on increases virus spread into a large number of species (Padidam *et al.,* 1999). Recombination events has negative effects on the quality of the reconstructed phylogenetic tree (Posada and Crandall, 2002; Ruths and Nakhleh, 2005). Hence recombination detection must be done to ensure accurate phylogenetic analyses and to understand parental type recombination and mechanisms of virus diversification.

Table 1: Countries from where leaf curl disease has been reported from Papaya.

S. No.	Country	Reference
1.	India	Thomas and Krishnaswamy (1939) Sen *et al*. (1946) Nariani (1956) Saxena *et al*. (1998) Raj *et al*. (2008) Singh-Pant *et al.* (2012) Varun *et al*. (2017) Nehra *et al*. (2019)
2.	Philippines	Chinte *et al.* (1959)
3.	Pakistan	Nadeem *et al.* (1997)
4.	China	Wang *et al.* (2004) Zhang *et al.* (2005) Huang and Zhou (2006)
5.	Taiwan	Chang *et al.* (2003)
6.	Bangladesh	Maruthi *et al.* (2007)
7.	Africa (Nigeria)	Taylor (2001)
8.	Vietnam	Ha *et al.* (2008)
9.	Oman	Ammara *et al.* (2015) Khan *et al.* (2012)
10.	Nepal	Shahid *et al.* (2013)
11.	Korea	Byun *et al.* (2016) Kim *et al.* (2018)

Table 2: Various full length begomoviral PLCV isolates reported from different host species other than papaya.

Sr. No.	Host	Accession Number	PLCV ISOLATE/STRAIN	Remarks
1.	*Ageratum conyzoides, Asteraceae*	NC_005321	Papaya leaf curl China virus -[G8] PaLCuCNV-G8	Wang *et al*. (2004)
2.	*Ageratum conyzoides, Asteraceae*	AJ811439	Papaya leaf curl China virus, isolate G7, PaLCuCNV-G7	Unpublished
3.	*Ageratum conyzoides, Asteraceae*	AJ558124	Papaya leaf curl China virus -[G8] PaLCuCNV-G8	Wang *et al.* (2004)
4.	*Ageratum conyzoides, Asteraceae*	KP685599	Papaya leaf curl China virus isolate JX01	Unpublished
5.	*Ageratum conyzoides, Asteraceae*	KC878474	Papaya leaf curl China virus isolate Vietnam14 segment DNA-A	Unpublished
6.	*Ageratum conyzoides, Asteraceae*	MF417766	Papaya leaf curl China virus isolate GX128	Unpublished
7.	*Ageratum conyzoides, Asteraceae*	MF417765	Papaya wangleaf curl China virus isolate BN3	Unpublished
8.	*Ageratum conyzoides, Asteraceae*	MF417764	Papaya leaf curl China virus isolate GD5	Unpublished
9.	*Ageratum conyzoides, Asteraceae*	KJ016238	Papaya leaf curl China virus isolate GX9	Unpublished
10.	*Ageratum conyzoides, Asteraceae*	KJ016234	Papaya leaf curl China virus isolate YS02	Unpublished
11.	*Ageratum conyzoides, Asteraceae*	AJ558125	Papaya leaf curl China virus - [G10]	Wang *et al*. (2004)
12.	*Ageratum conyzoides, Asteraceae*	AJ811439	Papaya leaf curl China virus isolate G7.	Unpublished
13.	*Ageratum conyzoides, Asteraceae*	JX294075	Papaya leaf curl China virus isolate ageratum segment DNA-A	Unpublished
14.	*Amaranthus cruentus, Amaranthaceae*	JN135233	Papaya leaf curl virus isolate Lucknow segment DNA-A	Unpublished
15.	*Calendula officinalis, Asteraceae*	MK087120	Papaya leaf curl virus isolate Cal-1	Unpublished
16.	*Calotropis procera, Apocynaceae*	JQ407224	Papaya leaf curl virus genomic sequence	Unpublished
17.	*Capsicum sp., Solanaceae*	KY978407	Papaya leaf curl virus isolate 249-1ISBD	Unpublished
18.	*Catharanthus roseus, Apocynaceae*	KX353619	Papaya leaf curl virus isolate DP1	Unpublished
19.	*Codiaeum variegatum, Euphorbiaceae*	MF278787	Papaya leaf curl virus Isolate AF14, Complete Genome	Unpublished
20.	*Corchoropsis timentosa, Malvaceae*	AJ876548	Papaya leaf curl China virus, isolate G43, PaLCuCNV-G43	Huang and Zhou (2006)
21.	*Crotalaria juncea, Fabaceae*	GQ200446	Papaya leaf curl virus [India:Pratapgarh1:2008] clone SHLD-NIFL-Pra-01	Unpublished
22.	*Crotalaria juncea, Fabaceae*	GQ200447	Papaya leaf curl virus	Unpublished

			[India:Pratapgarh1:2008] clone SHLD-NIFL-Pra-01	
23.	*Crotalaria juncea, Fabaceae*	GQ200448	Papaya leaf curl virus [India:Pratapgarh1:2008] clone SHLD-NIFL-Pra-01	Unpublished
24.	*Croton bonplandianum, Euphorbiaceae*	KM525657	Papaya leaf curl virus isolate CB1	Unpublished
25.	*Croton bonplandianum, Euphorbiaceae*	JN817517	Papaya leaf curl virus isolate CB1	Unpublished
26.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	KT253639	Papaya leaf curl virus isolate India-Valsad-Cluster bean1-2015	Unpublished
27.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	KT253647	Papaya leaf curl virus isolate India-Valsad-Cluster bean1-2015	Unpublished
28.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	LT009395	Papaya leaf curl virus complete genome, isolate Cluster bean, clone MNT-D18	Tahir *et al.* (2017)
29.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	LT009396	Papaya leaf curl virus complete genome, isolate Cluster bean, clone MNT-D18	Tahir *et al.* (2017)
30.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	LT009397	Papaya leaf curl virus complete genome, isolate Cluster bean, clone MNT-D18	Tahir *et al.* (2017)
31.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	LT009398	Papaya leaf curl virus complete genome, isolate Cluster bean, clone MNT-D18	Tahir *et al.* (2017)
32.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	LT009399	Papaya leaf curl virus complete genome, isolate Cluster bean, clone MNT-D18	Tahir *et al.* (2017)
33.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	LN845913	Papaya leaf curl virus complete genome, isolate Cluster bean, clone MNT-D18	Tahir *et al.* (2017)
34.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	LN845914	Papaya leaf curl virus complete genome, isolate Cluster bean, clone MNT-D18	Tahir *et al.* (2017)
35.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	LN845915	Papaya leaf curl virus complete genome, isolate Cluster bean, clone MNT-D18	Tahir *et al.* (2017)
36.	*Cyamopsis tetragonoloba*	LN845916	Papaya leaf curl virus complete genome, isolate Cluster bean, clone MNT-D18	Tahir *et al.* (2017)
37.	*(Cluster bean), Fabaceae*	LN845917	Papaya leaf curl virus complete genome, isolate Cluster bean, clone MNT-D18	Tahir *et al.* (2017)
38.	*Cyamopsis tetragonoloba*	LN845919	Papaya leaf curl virus complete genome, isolate Cluster bean, clone MNT-D18	Tahir *et al.* (2017)
39.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	KU514411	Papaya leaf curl virus complete genome, isolate Cluster bean, clone MNT-D18	Tahir *et al.* (2017)
40.	*Cape Gooseberry (Rasbhari)*	LT009400	Papaya leaf curl virus complete genome, isolate Cape gooseberry,clone MNT-SM86	Tahir *et al.* (2017)
41.	*Eclipta prostrata, Asteraceae*	AM691552	Papaya leaf curl China virus isolate F25, PaLCuCNV-F25	Unpublished
42.	*Eclipta prostrata, Asteraceae*	AM691553	Papaya leaf curl China virus, isolate LC1-2, PaLCuCNV-LC1-2	Unpublished
43.	*Euphorbia pulcherrima, Euphorbiaceae*	FJ495184	Papaya leaf curl Guangdong virus - [China:Fujian:Euphorbia:2006]	Cheng *et al.* (2014)
44.	*Eustoma grandiflorum, Gentianaceae*	LC089766	Papaya leaf curl Guandong virus DNA,	Unpublished
45.	*Glycine max (soybean), Fabaceae*	JN807765	Papaya leaf curl virus-[soybean: Lucknow]	Unpublished
46.	*Gossypium sp. (Cotton), Malvaceae*	AJ436992	Papaya leaf curl virus [Pakistan:Cotton:2002], PaLCuV-PK[PK:Cot:02]	Mansoor *et al.* (2003a)
47.	*Kalimeris indica /Aster alpinus (Aster), Asteraceae*	JQ954859	Papaya leaf curl virus isolate Aster Lucknow	Srivastava *et al.* (2013)
48.	*Lycopersicon esculentum (Tomato) cultivar Pusa Ruby, Solanaceae*	DQ629103	Papaya leaf curl virus [India:New Delhi:tomato:2005]	Unpublished
49.	*Lycopersicon esculentum (Tomato), Solanaceae*	AJ704604	Papaya leaf curl China virus, isolate G22, Pa:CuCNV-G22	Unpublished
50.	*Lycopersicon esculentum (Tomato), Solanaceae*	AJ558116	Papaya leaf curl China virus - [G12], PaLCuCNV-G12	Unpublished
51.	*Lycopersicon esculentum (Tomato), Solanaceae*	AJ558117	Papaya leaf curl China virus - [G30], PaLCuCNV-G30	Unpublished
52.	*Lycopersicon esculentum (Tomato), Solanaceae*	FN297834	Papaya leaf curl China virus GX4, PaLCuCNV-GX4	Zhang *et al.* (2010)
53.	*Lycopersicon esculentum (Tomato), Solanaceae*	EU874386	Papaya leaf curl China virus isolate ZM1, PaLCuCNV-ZM1	Unpublished

54.	*Lycopersicon esculentum (Tomato), Solanaceae*	FN256260	Papaya leaf curl China virus HeNZM1	Zhang *et al.* (2010)
55.	*Lycopersicon esculentum (Tomato), Solanaceae*	AM691554	Papaya leaf curl China virus DNA-A	Guo *et al.* (2015)
56.	*Lycopersicon esculentum (Tomato), Solanaceae*	LN878129	Papaya leaf Curl virus	Unpublished
57.	*Lycopersicon esculentum (Tomato), Solanaceae*	EU874386	Papaya leaf curl China virus isolate ZM1 segment DNA-A	Unpublished
58.	*Lycopersicon esculentum (Tomato), Solanaceae*	FN256260	Papaya leaf curl China virus HeNZM1 complete genome	Unpublished
59.	*Lycopersicon esculentum (Tomato), Solanaceae*	FN297834	Papaya leaf curl China virus GX4	Unpublished
60.	*Lycopersicon esculentum (Tomato), Solanaceae*	AJ704604	Papaya leaf curl China virus DNA A, isolate G22	Unpublished
61.	*Lycopersicon esculentum (Tomato), Solanaceae*	KR732665	Papaya leaf curl China virus isolate JZ2	Unpublished
62.	*Lycopersicon esculentum (Tomato), Solanaceae*	KR732666	Papaya leaf curl China virus isolate JZ2	Unpublished
63.	*Lycopersicon esculentum (Tomato), Solanaceae*	KR732667	Papaya leaf curl China virus isolate JZ2	Unpublished
64.	*Lycopersicon esculentum (Tomato), Solanaceae*	KR732668	Papaya leaf curl China virus isolate JZ2	Unpublished
65.	*Lycopersicon esculentum (Tomato), Solanaceae*	KR732669	Papaya leaf curl China virus isolate JZ2	Unpublished
66.	*Lycopersicon esculentum (Tomato), Solanaceae*	KR732670	Papaya leaf curl China virus isolate JZ2	Unpublished
67.	*Lycopersicon esculentum (Tomato), Solanaceae*	KR706485	Papaya leaf curl China virus isolate HNZM1	Unpublished
68.	*Lycopersicon esculentum (Tomato), Solanaceae*	KP195721	Papaya leaf curl China virus isolate GXHZ segment DNA-A	Unpublished
69.	*Lycopersicon esculentum (Tomato), Solanaceae*	JX555979	Papaya leaf curl China virus isolate JiaoZuo	Unpublished
70.	*Lycopersicon esculentum (Tomato), Solanaceae*	KU892657-77	Papaya leaf curl China virus isolate YL1, BS10, BS09	Unpublished
71.	*Lycopersicon esculentum (Tomato), Solanaceae*	JX128101	Papaya leaf curl China virus isolate GX89 segment DNA-A	Unpublished
72.	*Lycopersicon esculentum (Tomato), Solanaceae*	JX128102	Papaya leaf curl China virus isolate GX89 segment DNA-A	Unpublished
73.	*Lycopersicon esculentum (Tomato), Solanaceae*	GQ373254	Papaya leaf curl China virus segment DNA A,	Unpublished
74.	*Lycopersicon esculentum (Tomato), Solanaceae*	KU376493	Papaya leaf curl virus isolate CN2	Unpublished
75.	*Lycopersicon esculentum, (Cultivar Cherry tomato), Solanaceae*	DQ629102	Papaya leaf curl virus segment DNA A	Unpublished
76.	*Nicotiana glutinosa, (Tobacco), Solanaceae*	HM143914	Papaya leaf curl virus segment DNA A	Unpublished
77.	*Nicotiana sp., (Tobacco), Solanaceae*	GQ139516	Papaya leaf curl virus clone CPT coat protein gene	Kumar *et al.* (2009)
78.	*Nicotiana tabacum, Solanaceae*	DQ641700	Papaya leaf curl China virus, PaLCuCNV	Ha *et al.* (2008)
79.	*Nicotiana tabacum, Solanaceae*	FJ869907	Papaya leaf curl Guangdong virus -F11, PaLCuGzV-F11	Unpublished
80.	*Passiflora sp, Passifloraceae*	KC161184	Papaya leaf curl virus isolate PF1	Cheng *et al.* (2014)
81.	*Passiflora sp, Passifloraceae*	MN092343	Papaya leaf curl China virus isolate PaLCuCNV-GNPF, complete genome	Huang *et al.* (2020)
82.	*Physalis peruviana, Solanaceae*	LN845920	Papaya leaf curl virus complete genome, clone MNT-ND-36	Tahir *et al.* (2017)
83.	*Populus alba, Salicaceae*	KY926899	Papaya leaf curl virus isolate RM428	Unpublished
84.	*Raphanus sativus, Brassicaceae*	KY026597	Papaya leaf curl virus clone Rad07, Rad38	Kumar *et al.* (2021)
85.	*Raphanus sativus, Brassicaceae*	KY026598	Papaya leaf curl virus clone Rad07, Rad38	Kumar *et al.* (2021)
86.	*Raphanus sativus, Brassicaceae*	FJ593629	Papaya leaf curl virus clone Rad07, Rad38	Kumar *et al.* (2021)
87.	*Rhynchosia capitata, Fabaceae*	FM955601	Papaya leaf curl virus clone M168-9	Ilyas *et al.* (2010)
88.	*Rhynchosia capitata, Fabaceae*	FM955602	Papaya leaf curl virus clone M168-9	Ilyas *et al.* (2010)
89.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	KT253646	Papaya leaf curl virus isolate India-Gandhinagar1-Cluster bean-2015,	Unpublished

90.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	KT253645	Papaya leaf curl virus isolate India-Jamnagar2-Cluster bean-2015	Unpublished
91.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	KT253644	Papaya leaf curl virus isolate India-Jamnagar1-Cluster bean-2015	Unpublished
92.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	KT253643	Papaya leaf curl virus isolate India-Bhavnagar3-Cluster bean-2015	Unpublished
93.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	KT253642	Papaya leaf curl virus isolate India-Bhavnagar2-Cluster bean-2015	Unpublished
94.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	KT253641	Papaya leaf curl virus isolate India-Bhavnagar1-Cluster bean-2015	Unpublished
95.	*Cyamopsis tetragonoloba (Cluster bean), Fabaceae*	KT253640	Papaya leaf curl virus isolate India-Valsad-Cluster bean-2015	Unpublished
96.	*Cestrum nocturnum, Solanaceae*	MN839534	Papaya leaf curl virus isolate WA1 segment DNA-A, complete sequence	Lal *et al.* (2020)
97.	*Jatropha gossypiifolia, Euphorbiaceae*	MZ217773	Papaya leaf curl Guntur virus isolate GuWC10, complete genome	Unpublished

Table 3: PLCV betasatelllites reported from non-papaya host species.

Sr. No.	Host	Accession Number	PLCV ISOLATE/STRAIN	Remarks
1	*Vigna radiata (Grain Legumes), Fabaceae*	DQ118862	Papaya leaf curl beta [India:Chinthapalli:2005]	Unpublished
2	*Lycopersicon esculentum (Tomato), Solanaceae*	GU370715	Papaya leaf curl virus betasatellite isolate PRM	Unpublished
3	*Lycopersicon esculentum (Tomato), Solanaceae*	LN887901, LN878110-11	Papaya leaf curl betasatellite complete sequence, isolate RSJ	Unpublished
4	*Lycopersicon esculentum (Tomato), Solanaceae*	LN901454-61, LN878112	Papaya leaf curl betasatellite complete sequence, isolate RS214	Unpublished
5	*Lycopersicon esculentum (Tomato), Solanaceae*	KJ605112	Papaya leaf curl virus betasatellite isolate India:Bangalore:TC281:2010	Unpublished
6	*Lycopersicon esculentum (Tomato), Solanaceae*	KJ605113	Papaya leaf curl virus betasatellite isolate India:Bangalore:TC281:2010	Unpublished
7	*Lycopersicon esculentum (Tomato), Solanaceae*	MH577038	Papaya leaf curl betasatellite clone pTAD21	Unpublished
8	*Lycopersicon esculentum (Tomato), Solanaceae*	KX353620	Tomato yellow leaf curl Thailand betasatellite isolate DP2,	Unpublished
9	*Lycopersicon esculentum (Tomato), Solanaceae*	KU376494	Papaya leaf curl betasatellite isolate CN2B,	Unpublished
10	*Lycopersicon esculentum (Tomato), Solanaceae*	LN824093	Papaya leaf curl betasatellite	Unpublished
11	*Parthenium hysterophorus, Asteraceae*	JX987089	Papaya leaf curl betasatellite isolate NBRI	Kumar *et al.* (2016)_
12	*Parthenium hysterophorus, Asteraceae*	LN906595	Papaya leaf curl betasatellite, clone Par-B1	Unpublished
13	*Parthenium hysterophorus, Asteraceae*	MF683837	Papaya leaf curl betasatellite isolate 1027	Unpublished
14	*Parthenium hysterophorus, Asteraceae*	MF683836	Papaya leaf curl beta satellite isolate 1027	Unpublished
15	*Pseuderanthemum reticulatum, Acanthaceae*	MH819292	Papaya leaf curl betasatellite isolate Pst	Unpublished

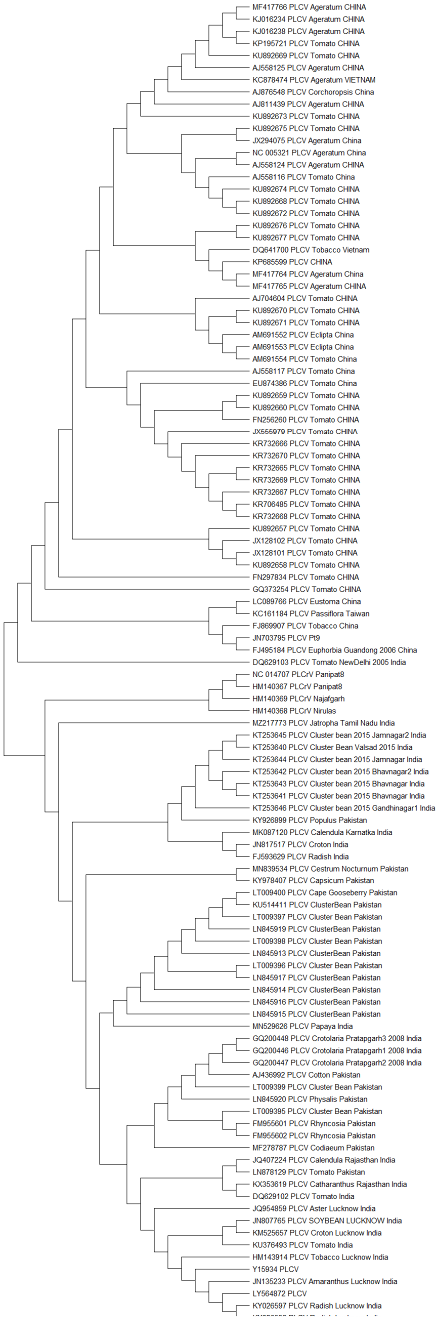

Fig. 1. The phylogenetic interrelationship inferred using the Maximum Likelihood method. The optimal tree is shown. The evolutionary distances were computed using the Maximum Composite Likelihood method. The rate variation among sites was modeled with a gamma +invariant (G+I) sites distribution. This analysis involved 109 nucleotide sequences. All ambiguous positions were removed for each sequence pair (pairwise deletion option). There were a total of 2937 positions (including gaps) in the final dataset. Evolutionary analyses were conducted in MEGA11 (Tamura *et al.,* 2021).

CONCLUSIONS AND FUTURE SCOPE

The host range is expanding at an alarming rate and this is true for almost all begomoviral complexes. The switching from being a specialist to a generalist requires immediate attention for developing strategies to ensure that the virus remains restricted and limited to fewer host and shorter stretches of phytogeographical regions. The expansion of viral strains from papaya to agricultural crops and vice-versa is becoming increasingly common which indicates general expansion in the host range which might be contributed also by the host expansion on which the vector whitefly feeds on, thus enabling the virus to spread far and wide, and providing more chances of recombination than ever. Furthermore, begomoviral complexes are showing recombination events frequently occurring in nature beginning from mixed infection as well as by general crossover events where parental strains recombine to produce more virulent strains against which the host plants are highly susceptible. Such rapid genomic changes are detrimental to agricultural crops. This study presents a succinct review on the current scenario of begomoviral complexes reported in the sequence database and their inter-relatedness among them. The results obtained clearly show clustering of strains primarily based on geographical proximity, followed by host specificity. This kind of clustering supports that within a geographical region the viral strains are infecting larger group of plant families attributed to both vector expansion of host and recombination events. Further research is required to be done in the aspects of strategies for development of mechanism of resistance in host plants as well as in viral genome and evolution, to help understand how host plants can be reinforced with sufficient strategies to cope with the increasing prevalence of viral infection and thus enabling the farmers to effectively control the disease spread.

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Contributed data or analysis tools and performed the analysis. All the authors contributed equally to prepare the manuscripts to its current shape.

Ethical Statement: No viral strain was isolated in this study or taken or maintained from any where. The authors declare that all ethical standards were taken care of while preparing the manuscripts.

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