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RESEARCH ARTICLE

Molecular characterisation and evolutionary analysis of Papaya ringspot virus infecting papaya (*Carica papaya* L.)

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Abstract

Papaya (*Carica papaya* L.) is a tropical, commercial fruit with high nutritive and medicinal value. Papaya ringspot virus (PRSV) causes destructive disease in papaya and cucurbit cultivation worldwide. The current study analysed the genetic diversity and phylogenetic relationship of 115 PRSV isolates submitted until December 2024 in NCBI, including one complete genome sequences from Palampur, India characterized in this study. The complete genome of a PRSV Palampur isolate collected during March 2020 from foothills of Himalayan region in northern India was characterized. The Palampur isolate (MW030522.1) showed close identity of 90 % with Bangladesh isolate (MH397222). Species demarcation analysis of nucleotide sequence revealed one major peak ranging between 79–85 %. The nucleotide diversity of the PRSV genome was 0.13. The 5' end of the genome containing the P1 gene showed high levels of polymorphism. Phylogenetic analysis showed 4 major groups (G1-G4) and one recombinant isolate (MH444652). The results suggest that the geographic region, rather than hosts, is the probable factor determining the genetic diversity of PRSV isolates. Neutrality tests and dN/dS ratio showed negative values, indicating purifying selection. The current study deepens understanding of PRSV genetic diversity and evolution, which can be used for development of effective management strategies against PRSV.

Keywords: *Carica papaya*; genetic diversity; papaya ringspot virus; phylogenetic analysis; molecular characterisation

Introduction

Papaya (*Carica papaya* L.), a member of the Caricaceae family, is widely cultivated in tropical and subtropical regions. It is widely known for its fruit and the production of papain, pectin and its medicinal properties, papaya is a critical crop in many parts of the world. Papaya is the third most cultivated tropical fruit. India stands as the largest producer, accounting for nearly 43 % of global papaya production. Brazil and India are the leading producers (1). Papaya is also highly valued for its exceptional nutritional content, being rich in vitamin A, vitamin C, potassium, folate and other essential nutrients, which makes it one of the most nutritionally dense fruits (2).

Papaya ringspot disease (PRSD), caused by the Papaya ringspot virus (PRSV), is a significant threat to papaya crops worldwide. First identified in Hawaii in the 1940s, PRSV rapidly spread across the globe, with its distribution now spanning 42 countries (3–5). In India, PRSV was first reported in the 1960s and the disease continues to be a major concern among farmers in various countries (6). The virus affects not only papaya but also cucurbits, causing substantial losses in these crops as well (7). Papaya ringspot virus is transmitted by aphids such as *Myzus persicae* and *Aphis gossypii* in a nonpersistent manner, spreading easily between plants (8). The virus can be classified into 2 main groups based on its host range: the papaya-infecting PRSV-P and the non-papaya infecting PRSV-W. These 2 groups are distinguished primarily by their ability to infect specific host species, with PRSV-P infecting papaya and cucurbits, whereas PRSV-W infecting only cucurbits (5, 7). The main factors influencing disease spread involve the amount of initial virus inoculum in papaya and other unknown hosts of PRSV, the status of aphids as transient vectors, variations in their life cycles, behaviour, ability to transmit the virus and effect of environmental factors on aphid population dynamics (9). Epidemiological studies are relevant for virus disease incidence to design the management strategies which affect virus transmission by vectors. The virus has been reported to infect plants in 7 families, including *Caricaceae, Cucurbitaceae, Fabaceae, Asteraceae, Araceae, Malvaceae* and *Solanaceae,* impacting a wide range of crops beyond papaya. In papaya, PRSV leads to characteristic symptoms such as mosaic patterns on leaves, wet-oily streaks on the petiole and trunk and distortion of young leaves. The infected fruit show ringspots and bumps, which can result in a reduction in fruit yield by 50 % or more, severely impacting production. Early detection and management of PRSV infection are crucial to minimize crop losses.

Several approaches exist for managing plant viral diseases, but the most sustainable and eco-friendly method remains the development of virus-resistant varieties. This approach has been particularly effective in papaya, where transgenic varieties resistant

to PRSV have been developed using the replicase and coat protein (CP) genes. However, resistance is not absolute, as new and more virulent strains of PRSV have occasionally overcome the resistance of genetically modified varieties (10). Therefore, continued research is needed to understand the genetic diversity of the virus and to develop more effective control measures.

Papaya ringspot virus belongs to the genus *Potyvirus* and its genome consists of a positive-sense, single-stranded RNA. The virus is transmitted by aphids and is characterized by its flexuous, filamentous virion structure (11). The genome encodes a single Open Reading Frame (ORF), which is translated into a polyprotein that is processed into 10 distinct proteins, including the CP, which encapsidates the viral RNA (12). Whole genome sequencing of PRSV isolates plays an essential role in understanding the evolution of virus, genetic diversity and geographic spread. In this study, we have characterized the complete genome sequence of a PRSV isolate from Palampur, India, located in the foothills of the Himalayas and analysed the evolutionary patterns of PRSV isolates, which provided critical insights into the virus's genetic composition, evolutionary trajectory and the potential implications for future control strategies.

Materials and Methods

Complete genome sequencing

Papaya leaf samples showing symptoms of mosaic pattern on the lamina, shoestring and distortion of young leaves, were collected from Palampur, Himachal Pradesh. Total RNA was extracted from leaf tissues using RNeasy Plant Mini kit (Qiagen, USA). The complete genome of the PRSV Palampur isolate was obtained as four overlapping amplicons using PrimeSTAR GXL Taq polymerase (Takara, Japan), following primer walking strategy. Four primer pairs were designed based on full length PRSV sequences obtained from NCBI (Table 1). PCR amplicons were cloned into the pGEM-T Easy Vector (Promega, Madison, WI) and transformed into *Escherichia coli* DH5α competent cells. The clones were sequenced using Sanger sequencing strategy. The complete genome sequences of the PRSV isolates were aligned using ClustalW. The full-length nucleotide sequences of the PRSV Palampur isolate were aligned with PRSV sequences available in the NCBI database using BioEdit version 7.2.5. The full-length nucleotide sequences of the PRSV Palampur (MW030522) were confirmed by NCBI BLAST analysis.

Sequence datasets and genetic diversity analysis

A total of 114 PRSV complete genome sequence downloaded from NCBI and an isolate from this study were used for sequence analysis. Multiple alignments of nucleotide sequences for individual genes and complete genome were performed using ClustalW in BioEdit version 7.2.5. The pairwise percent nucleotide sequence identity matrix was carried out using SDT 1.2. DnaSP v. 6.0 was utilized to calculate various parameters to investigate nucleotide polymorphism. Using a sliding window size of 100 bp and a step size of 25 bp, DnaSP v5 software was used to determine nucleotide diversity (Pi) across 115 PRSV complete genomes. Genetic diversity was assessed by estimating the total of mutations (η), nucleotide diversity (Pi), average number of nucleotide differences (K), number of haplotypes (H), haplotype diversity (HD).

Phylogenetic and evolutionary analysis

The evolutionary history was inferred using the Neighbor-Joining method, with bootstrap support (1000 replicates) indicated by the percentage of replicate trees in which the associated taxa clustered together next to the branches. Evolutionary analyses were performed in MEGA11. Neutrality tests were performed using Tajima's D, Fu and Li's D* and Fu and Li's F* tests available in DnaSP v. 6.0. The non-synonymous to synonymous substitution ratio (dN/dS) was also calculated using standard parameters in Datamonkey Adaptive Evolution Server for each dataset, with ratios greater than 1 indicating positive (diversifying) selection pressure, ratios less than 1 indicating negative (purifying) selection pressure and ratios equal to 1 indicating neutral selection pressure. The identification of sites subject to positive and negative selection was achieved using the fixed-effects likelihood (FEL) method implemented in DataMonkey (www.datamonkey.org).

Results

Host range and geographical distribution

The geographical distribution and occurrence of PRSV was determined using 1953 PRSV sequences submitted to NCBI database until December 2024. PRSV have been reported from 42 countries across world and known to infect plants from seven families: Caricaceae (*Carica papaya*, *Vasconcellea cauliflora*, *Vasconcellea* x *heilbornii*), Cucurbitaceae (*Benincasa hispida, Citrullus colocynthis, Citrullus lanatus, Coccinia grandis, Cucumis anguria, Cucumis dipsaceus, Cucumis melo, Cucumis metuliferus, Cucumis sativus, Cucurbita maxima, Cucurbita moschata, Cucurbita pepo, Fevillea trilobata, Lagenaria siceraria, Luffa aegyptiaca, Melothria pendula, Momordica charantia, Sicyos edulis, Siraitia grosvenorii, Trichosanthes anguina, Trichosanthes cucumerina, Trichosanthes cucumeroides*). Solanaceae (*Capsicum annum, Solanum tuberosum*), Fabaceae (*Clitoria ternatea, Pisum sativum, Robinia pseudoacacia, Vigna vexillata*), Araceae (*Colocasia esculenta*), Malvaceae (*Corchorus olitorius*), Asteraceae (*Parthenium hysterophorus, Xanthium strumarium*) (Fig. 1).

Genetic diversity

Genetic diversity was analysed using the complete nucleotide sequences of 115 PRSV isolates. The species demarcation tool (SDT) was used to determine the boundaries between the isolates based on the identities between the nucleotide sequences. The pairwise identities of PRSV isolates ranged from 75.2–90.7 %. However, the matrix graph produced by the analysis revealed one major peak ranging between 79–85%, indicating the species demarcation (Fig. 2). Based on an identity cutoff of 85 %, identity scores were assigned

Table 1. Primers used for the cloning of Papaya ringspot virus complete genome

Primer name	Sequence (5'-3')	Primer position	Amplicon size (bp)
YM11F	AAATAAAACATCTCAACACAACACAATT	1-885	885
YM12R	TTCRAGTGCTAGRTGCACTGC		
YM19F	CAGTTGCTAGTGGAGTCATTGG	757-4395	3638
YM20R	CTCGAACGTGACATCTATAGGC		
YM15F	GTGGAYAAGAGTGAYTGTGTTTA	4203-6977	2774
YM16R	GAAGCTATRCCATTGTARTTYCTCAT		
YM17F	ATGAGRAAYTACAATGGYATAGCTTC	6951-10317	3366
YM18R	CTCTCATTCYAAGAGGCTCGAATA		

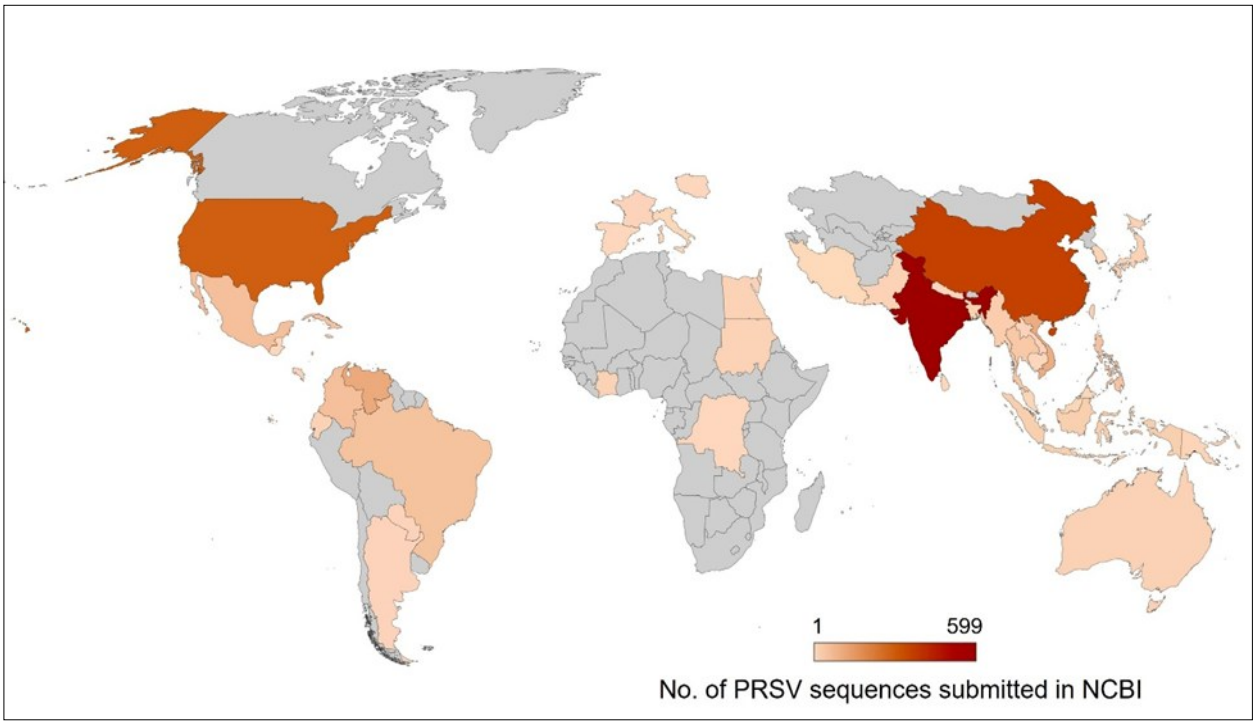

Fig. 1. Global distribution of Papaya ringspot virus isolates.

to all 115 isolates, revealing four distinct groups and one recombinant isolate (Supplementary Table 1).

The Palampur isolate (MW030522.1) showed close identity of 90.7 % with Bangladesh isolate (MH397222.1). Less identity of 75.2 % with Bangladesh isolates, MH444652.1 followed by 79.3 % with China isolate (MK988418.1).

The DnaSP v5 software was utilized to evaluate the nucleotide diversity (Pi) throughout the entire PRSV genome. A total of 8737 mutations were identified across 5555 sites, with an average of 1363.18 nucleotide differences between sequences (k). The maximum number of mutations was found in P1 gene (2278) followed by Nib gene (1359). The nucleotide diversity (Pi) across the genome was calculated to be 0.13. Among the ORFs P1 gene had the highest nucleotide diversity of 0.23, with an average number of nucleotide differences of 370.9. The number of haplotypes across 115 PRSV isolates was 109. Analysis based on the ten coding regions revealed a range of values, with 83 haplotypes in 6K1 to 104 in the P1/Hc-Pro gene.

The haplotype distribution of the whole genome was 0.9989 and it was close to that of the P1 gene, which had a value of 0.9980, indicating high genetic variation within the P1 gene (Table 2). The 5' end of the genome (~up to 2000) corresponding to P1 gene displayed high levels of polymorphism in comparison to other genes (Fig. 3).

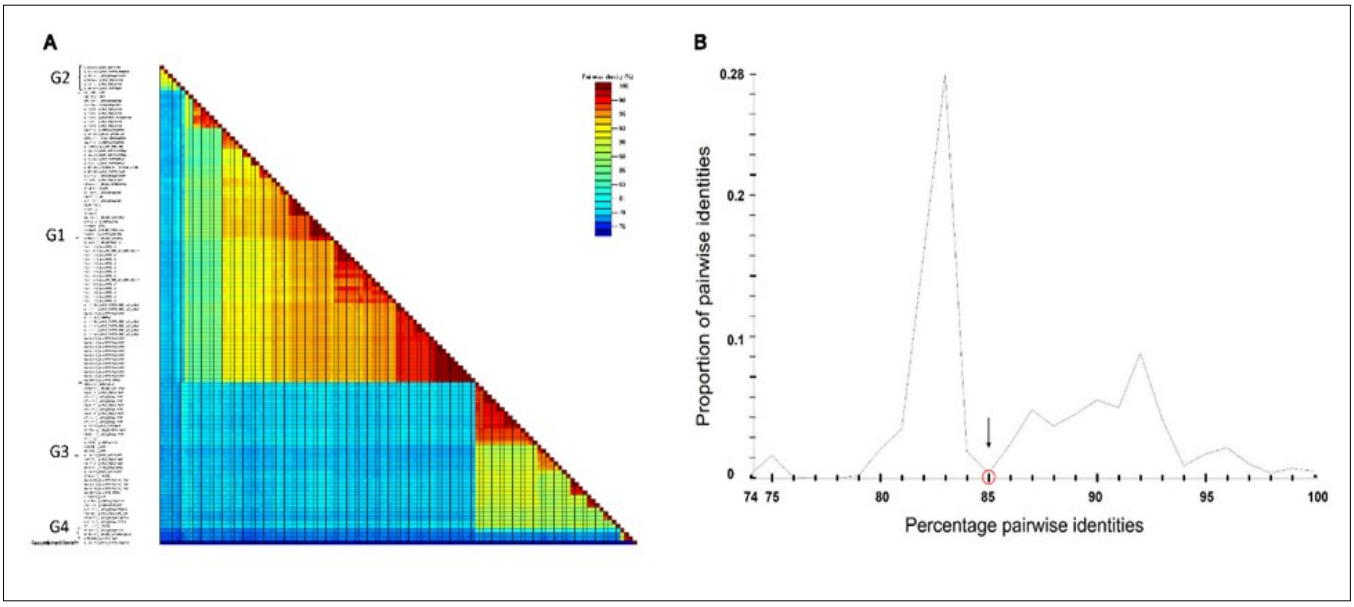

Fig. 2. Species demarcation tool (SDT) interface.

A) Colour-coded matrix of pairwise identity scores generated from nucleotide sequence comparisons. Each cell represents the degree of sequence similarity between two sequences, with colour intensity corresponding to percentage identity, B) Distribution plot of pairwise identity scores. The valleys between peaks represent ranges of percentage identities that serve as relatively conflict-free boundaries for establishing taxonomic demarcation thresholds. The arrow indicates the 85 % pairwise identity threshold, commonly used as a cutoff for taxonomic demarcation.

Table 2. Genetic diversity of Papaya ringspot virus

	⊠, Eta, number of mutations	Pi, Nucleotide diversity	K, Average number of nucleotide differences	H, Number of Haplotypes	HD
Complete genome	8737	0.13707	1363.185	109	0.9989
P1	2278	0.23096	370.925	104	0.9980
Hc-Pro	1028	0.11724	160.614	104	0.9982
P3	813	0.11792	122.042	99	0.997
6K1	120	0.11687	18.232	83	0.988
CI	1416	0.11459	218.295	103	0.9977
6K2	150	0.11450	19.466	87	0.994
VPg	454	0.13407	76.017	91	0.994
Nia-Pro	574	0.13197	94.229	97	0.997
Nib	1359	0.13656	219.186	99	0.997
CP	544	0.07873	64.004	96	0.996

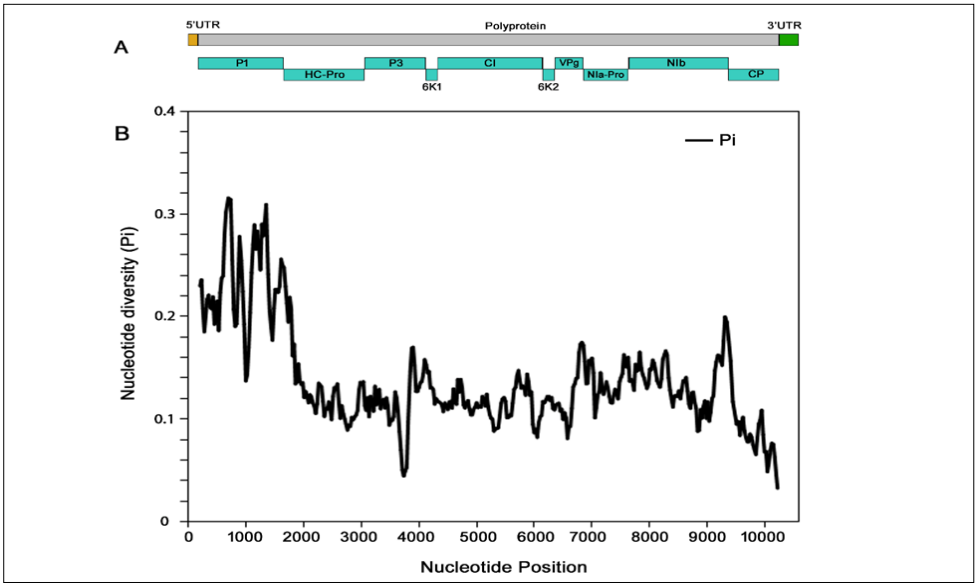

Fig. 3. Nucleotide diversity graph of 115 papaya ringspot virus genome sequences.

A) Graphical representation of Papaya ringspot virus genome, B) The graph shows the nucleotide diversity across the viral genome. Pi is the average number of nucleotide differences per site.

Phylogenetic analyses

The phylogenetic tree analyses of PRSV divided the isolates into 4 major groups (G1-G4) whereas one recombinant isolate (MH444652) acquired an independent position in the phylogenetic tree (Fig. 4). The grouping pattern was consistent with the results of the SDT analysis, which also revealed 4 groups and one recombinant based on the 85 % nucleotide identity threshold. The consistency between phylogenetic and SDT analyses reinforces the validity of the 85 % cutoff as a criterion for species or group demarcation among PRSV isolates. The analysis showed that the isolates are geographically conserved rather than host specific. The Palampur isolate was found in G2. The PRSV isolates had an overall mean nucleotide identity of 84 %.

Population selection and expansion

Neutrality tests (Tajima's D, Fu and Li's D and Fu and Li's F) were conducted to investigate whether demographic forces or selection are influencing the PRSV population. The analysis of the complete genome revealed negative values for all tests, indicating purifying selection and population expansion. Similarly, negative values were observed for all genes when tested with Tajima's D, Fu and Li's D and Fu and Li's F, suggesting that purifying selection and population expansion have likely played a significant role in shaping the population's genetic diversity. The consistent negative values across these tests further support the conclusion that the PRSV population is undergoing purifying selection.

The calculated dN/dS ratio using MEGAx was less than 1, ranging between 0.08 and 0.52, across the genome and including all gene. These results indicate the negative selection. Additionally, a fixed effects likelihood (FEL) analysis was conducted for all genes to infer non-synonymous (dN) and synonymous (dS) substitution rates on a per-site basis, using the given coding alignment and corresponding phylogeny. The CI gene showed a maximum of 580 amino acids under negative selection, whereas P1 gene showed 3 amino acids and P3 gene showed four amino acids under positive selection, representing diverse selection. In contrast, all other genes showed negative or purifying selection, demonstrating the prevalence of purifying selection in PRSV (Table 3).

Discussion

Papaya (*Carica papaya* L.) is a significant tropical fruit crop cultivated globally, valued for its economic and nutritional benefits. However, papaya cultivation faces a major threat from PRSV, which is recognized as one of the most destructive viral pathogens affecting papaya production worldwide (12, 13). PRSV was first detected in Oahu Island in 1940s PRSV is a highly transmissible virus that causes rapid disease progression, often leading to near-total yield losses within a few months of infection (5, 14, 15). This viral disease not only impacts papaya production but also poses a substantial threat to the economies of countries that rely on papaya as a staple crop (16–18). Management of PRSV through intensive rogueing and vector control is technically feasible; however, it is not economical nor eco-

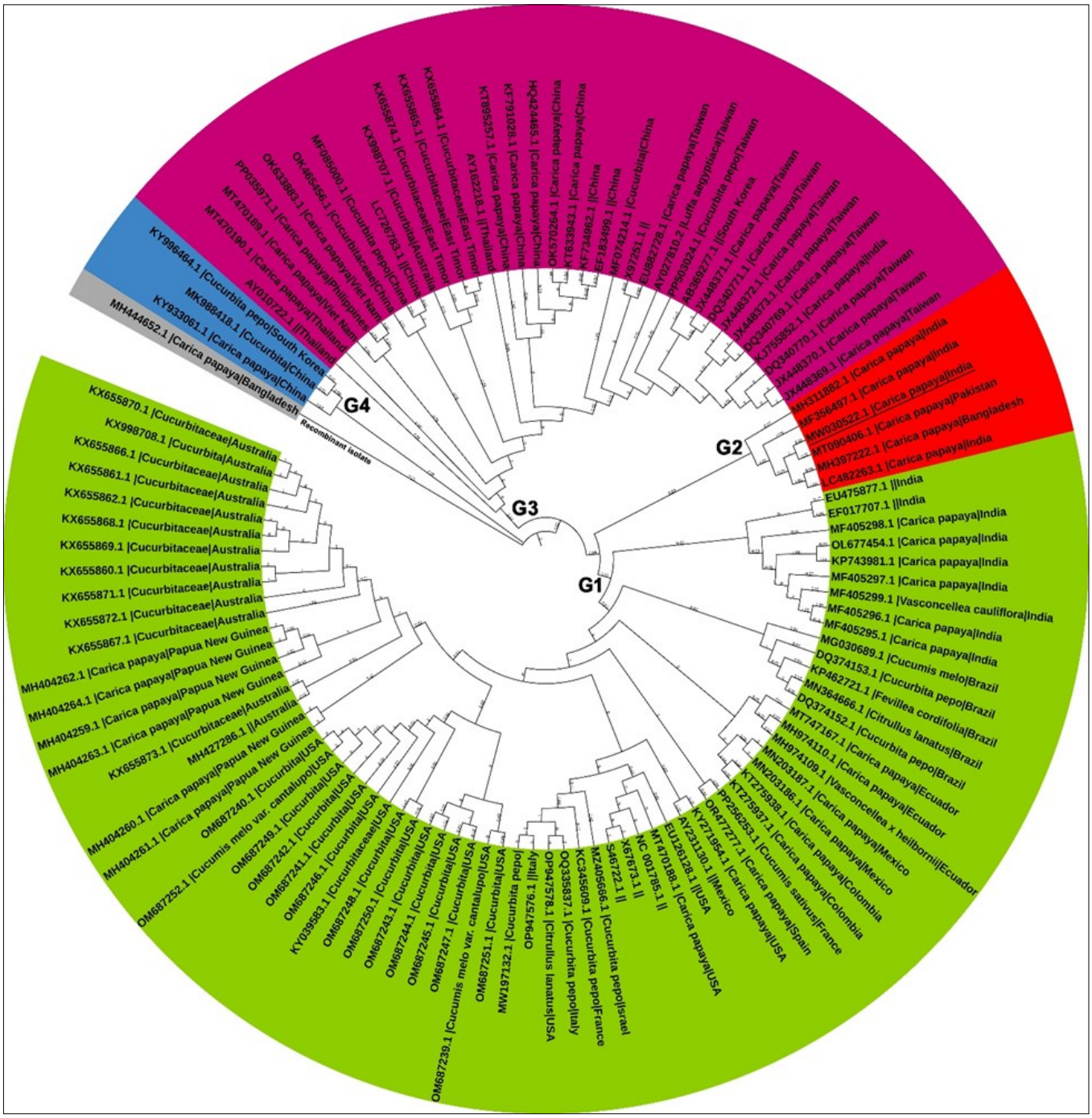

Fig. 4. Evolutionary analyses of 115 full-length papaya ringspot virus genome sequences. Neighbor-net reconstruction of relationships among full genome sequences of PRSV. The consensus tree was obtained using MEGA11 software. The PRSV isolate from this study is underlined.

Table 3. Neutrality tests and selection pressure analysis of Papaya ringspot virus

Virus component	Tajima's D	Fu and Li's D	Fu and Li's F	*dn/ds*	Total number of amino acid sites under FEL	
					AA under positive/ diversifying selection	AA under negative/ purifying selection
Complete genome	-0.57497	-0.90364	-0.90134	Na	Na	Na
P1	-0.45219	-0.26904	-0.42248	0.52	3	365
Hc-Pro	-0.56912	-0.92520	-0.91362	0.20	0	400
P3	-0.67801	-0.79693	-0.88970	0.40	4	266
6K1	-0.62777	-0.80397	-0.87253	0.12	0	42
CI	-0.60691	-1.14274	-1.07534	0.08	0	580
6K2	-1.01941	-1.04966	-1.24328	0.09	0	48
VPg	-0.36693	-0.63794	-0.61754	0.08	0	172
Nia-Pro	-0.42602	-1.17919	-1.00340	0.16	0	213
Nib	-0.47930	-1.19901	-1.04224	0.25	0	460
CP	-1.25508	-1.96136	-1.96624	0.13	0	192

friendly (19). Cross protection with mild PRSV strain confers only limited protection (20, 21). PRSV has been reported in 42 countries and infects plants from seven distinct botanical families, including Caricaceae, Cucurbitaceae, Fabaceae, Asteraceae, Araceae, Malvaceae and Solanaceae. The broad host range of the virus further complicates efforts to manage its spread.

In the present study, the complete genome of PRSV was characterized from papaya plants grown in the northern Himalayan region of India, a region that has not been extensively studied with respect to PRSV genetic diversity. Phylogenetic analysis of the complete genome nucleotide sequences of 115 PRSV isolates revealed clear clustering of isolates based on their geographic origin, this suggests that local spread within regions may be a significant factor in the distribution of the virus (22). Isolates from North America, South America and Europe were grouped together in a single clade, suggesting a historical link in the movement of plant material between these regions (18, 23). Conversely, PRSV isolates from India showed considerable genetic divergence, clustering into 3 distinct groups (G1-G3). This indicates the presence of a high level of genetic variability among Indian PRSV isolates, likely driven by factors such as host adaptability, environmental conditions and the ability of virus to rapidly evolve (24).

The PRSV isolate from Palampur, located in the northern Himalayan region of India, was found to share a high degree of sequence identity with other Indian isolates and the Bangladesh isolate (MH397222). This suggests that the Palampur isolate may be closely related to other regional strains, reflecting the genetic continuity and shared evolutionary pattern of PRSV isolates in this part of South Asia. This genetic proximity also supports the notion that PRSV in India may have evolved through local recombination events, contributing to the observed genetic diversity within the region (25). Additionally, the geographic separation of PRSV isolates observed in the phylogenetic analysis highlights the impact of regional factors such as host plant species, vector populations and climatic conditions on the evolution of the virus.

Population genetic analyses further revealed strong signatures of purifying selection acting across the PRSV genome, as indicated by consistently negative neutrality test values and low dN/dS ratios. The dominance of purifying selection, together with limited site-specific positive selection in genes such as P1 and P3, reflects a balance between functional constraint and adaptive evolution, a pattern commonly observed among potyviruses (23, 26), including recent population-level analyses of PRSV (27).

The findings of this study align with previous research that indicates a higher level of genetic diversity in Indian PRSV isolates compared to isolates from other regions (17, 18, 28). This could be due to the lack of resistant varieties, the rapid evolution of new viral strains through recombination (29) and the diverse aphid species present in India that act as vectors for the virus (10). The genetic divergence of PRSV isolates in India may contribute to the complexity of managing the disease, as different strains may exhibit varying degrees of virulence and host specificity.

Conclusion

This study provides valuable insights into the genetic diversity and evolutionary dynamics of PRSV, particularly in the context of India's papaya-growing regions. The close genetic relationship between the Palampur isolate and other Indian and Bangladesh isolates reinforces the idea of regional adaptation and suggests that local strains of PRSV may be more genetically stable within specific geographic areas. However, the broader genetic variability observed among Indian isolates highlights the ongoing challenges in controlling the disease and developing resistant varieties. As the virus continues to evolve, it is crucial to consider the role of genetic diversity, climate and host interactions in shaping PRSV populations, which will ultimately inform more effective disease management strategies and the development of resistant papaya cultivars.

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Authors' contributions

SB, YM and VS contributed to data analysis, design and preparation of the original draft. VS, NPMP, SK and CM contributed for draft review and writing. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

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