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RESEARCH ARTICLE

Transmission dynamics of mungbean yellow mosaic virus (MYMV) in blackgram: Vector and seed perspectives

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Abstract

Mungbean yellow mosaic virus (MYMV), a devastating begomovirus transmitted by the whitefly (*Bemisia tabaci*), is a major constraint in blackgram (*Vigna mungo*) production across India. The present study aimed to assess the spatial distribution of MYMV disease incidence, confirm the viral identity through molecular diagnostics, investigate vector transmission efficiency and evaluate the seed-transmissible nature of MYMV in blackgram cultivar CO 5. Field surveys in Tamil Nadu during 2023 revealed disease incidence ranging from a minimum of 45 % at Sukkampatti, Madurai, to a maximum of 78 % at Narasipuram, Coimbatore. PCR analysis with *CP, MP* and *REP* genes confirmed the presence of MYMV in all field-collected samples, with sequences submitted to NCBI (PQ384577, PV500803 and PV500802). Transmission of MYMV with whitefly Asia I genotype recorded a maximum transmission efficiency of 87.5 % and 93.75 % at 24 hr acquisition access periods (AAP) and inoculation access periods (IAP) respectively, with consistent symptom expression and was further confirmed with PCR. In a grow-out test conducted with field-collected seeds from infected plants, the plants were symptomless, but 51 % of the tested plants were positive in PCR. The dissected seed parts from these PCR positive first-generation grow-out test plants indicated the presence of MYMV in 100 % of seed coats, 80 % of cotyledons and embryonic axes. A second grow-out test conducted with 25 seeds from first-generation PCR-positive plants was again asymptomatic and 40 % of plants were PCR positive. These results provide strong evidence of asymptomatic, latent MYMV infections that act as cryptic inoculum for whitefly-mediated spread. These findings emphasize the need for integrated disease management strategies, including seed certification, molecular diagnostics and early whitefly control to limit MYMV spread and ensure virus free seed production in blackgram.

Keywords: Acquisition access period; *Bemisia tabaci*; blackgram; embryonic axes; inoculation access period; MYMV; PCR

Introduction

Blackgram (*Vigna mungo* (L.) Hepper) is a vital pulse crop cultivated extensively across India, occupying approximately 4.63 million hectares with a total production of 2.78 million tonnes and an average productivity of 987 kg ha^{-1}. In Tamil Nadu, blackgram is cultivated in an area of 4.07 lakh hectares, contributing 2.69 lakh tonnes with an average productivity of 660 kg ha^{-1} (1). Despite its agronomic and nutritional importance, the productivity of blackgram remains below its genetic potential, primarily due to a range of biotic stresses. In recent decades, plant viruses, particularly begomoviruses, have caused recurrent epidemics and severe yield losses in agricultural ecosystems, owing to their rapid evolution and adaptation to global climatic changes driven by intense selection pressures (2). Among these, yellow mosaic disease (YMD), caused by mungbean yellow mosaic virus (MYMV), poses the most severe threat, significantly impacting both yield and quality. Such seed association poses significant phytosanitary risks, as infected seed can facilitate long-distance dissemination of the virus through the international seed trade, bypassing vector-mediated barriers. Unlike horizontal transmission via whitefly vectors, which limits spread to local agro-ecological zones, vertical (seed) transmission could enable MYMV to establish in new, distant regions, thereby intensifying its threat to global legume production (3, 4).

MYMV is a single-stranded DNA virus classified under the genus *Begomovirus*, family Geminiviridae. First reported from mungbean fields in New Delhi (5). The virus is characterized by the development of small yellow specks on leaf lamina that progressively lead to complete leaf chlorosis, reduced flowering, malformed pods and poor seed development (3). The whitefly, *Bemisia tabaci* (Gennadius), is one of the most destructive insect pests affecting tropical and subtropical regions worldwide (6). It is a highly polyphagous pest, believed to have originated in India and is known to infest over 700 plant species, including numerous agriculturally and horticulturally significant crops (7). Current research has revealed that *B. tabaci* comprises a complex of at least 34 genetically distinct yet morphologically indistinguishable cryptic species or subgroups (8-10). *B. tabaci*

Asia II 1 predominates in Northern India, while Asia II 8 is dominant in Southern India, with stable virus-vector associations across regions (8). MYMV-urdbean strains prevail in the North, MYMV-vigna in the South and MYMV in Eastern India.

The invasive *B. tabaci* MEAM1 was first reported in India from tomato in Kolar district, with subsequent findings also mainly restricted to tomato in the same region and one report from Dabhoi in western India (10-14). Despite its generally broad host range, MEAM1 in India appears to show a preference for solanaceous hosts, as it has rarely been detected on legumes and it was absent in surveys focused on leguminous crops (9). These observations, together with its limited distribution, indicate that the earlier suggestion of rapid MEAM1 invasion in South India may not have materialized and to date there is no report of the invasive MED in India. Virus surveys over consecutive years further revealed region-specific predominance of yellow mosaic virus strains: MYMV-urdbean in *V. radiata, V. mungo* and *Glycine max* in northern India, MYMV-vigna in southern India and MYMV in the east, consistent with earlier reports (15-17). These genetic groups exhibit notable variation in key biological traits, such as host plant range, insecticide resistance, dispersal capacity, virus transmission efficiency and esterase activity patterns (18-20).

The whitefly highly efficient vector, capable of transmitting 114 plant virus species across several genera. Notably, approximately 90 % of these viruses belong to the genus *Begomovirus*, while the remaining are distributed among *Carlavirus, Crinivirus, Closterovirus* and *Ipomovirus* genera (19, 21). This pest causes significant yield losses both directly, by sucking plant sap and indirectly, by transmitting viral diseases, particularly those caused by viruses in the genus *Begomovirus* (18). MYMV is transmitted in a circulative and persistent manner by the whitefly *B. tabaci*, involving ingestion, translocation through the insect's midgut and hemolymph and release into host plant tissues through salivary secretions (22). While even a single whitefly can acquire and transmit the virus to plants, female *B. tabaci* are generally more effective and active in virus transmission than their male counterparts. A single viruliferous whitefly could transmit the virus, while ten whiteflies per plant ensured 100 % transmission (23). The minimum acquisition and inoculation access periods required were 15 min each, with complete transmission achieved at 12 hr. Although this transmission cycle is well understood, many unanswered intricacies remain about the virus's replication within the vector and the possibility of vertical (transovarial) transmission.

Most plant viruses spread from one plant to another through insect vectors or contact with infected sap, which is known as horizontal transmission (24). However, some viruses can also be spread through infected seeds (25). This type of transmission is more serious because it allows the virus to pass from one generation to the next. Unlike insect transmission, seed -borne viruses can survive for longer periods and travel across regions, even without the presence of vectors. As a result, seed transmission helps viruses overcome geographical and seasonal limitations, making them harder to control. Until recently, begomoviruses were thought to be non-seed transmissible. However, mounting evidence has begun to challenge this assumption. Recent studies have documented seed transmission in several begomoviruses, such as sweet potato leaf curl virus (SPLCV) in sweet potato, MYMV in blackgram, bitter gourd yellow mosaic virus (BgYMV) in bitter gourd, dolichos yellow mosaic virus (DoYMV) in lablab, ToLCNDV in bitter gourd and chayote (26-32). The early appearance of YMD symptoms on the first trifoliate leaf in field-grown blackgram further supports the hypothesis of seed-borne transmission (27). The seed-borne nature of MYMIV in mungbean cultivars Pusa 1371 and Pusa 9531 using DAC-ELISA, PCR and progeny tests across three seasons (33). Low ELISA absorbance and inconsistent PCR amplification were observed only in whole seeds and seed coats, not in cotyledons or embryonic axes. Seedlings raised from infected seeds tested negative for MYMV and showed no visible symptoms. The study concluded that MYMV may be seed-borne but is not seed-transmitted in the tested cultivars. MYMV detected in all the three parts of the seeds of blackgram, such as seed coat, cotyledon and embryo (34).

Based on these studies, a more comprehensive understanding of MYMV transmission dynamics is urgently required for disease management. Therefore, the present study aims to investigate MYMV dissemination through horizontal and vertical transmission by whitefly vectors and seed in blackgram, providing crucial insights into the virus's epidemiology and potential strategies for sustainable disease control.

Materials and Methods

Documentation and collection of mungbean yellow mosaic disease symptoms

Blackgram leaf samples showing mosaic symptoms were collected from major blackgram-growing regions of Tamil Nadu during 2023. The locations included Vellimalaipattinam and Narasipuram villages of Coimbatore district, the Agricultural College and Research Institute in Coimbatore and Kudumiyanmalai and Sukkampatti in Madurai district. During the collection, the type of symptoms observed, whitefly population and percent disease incidence of YMD were recorded (Table S1). Whitefly populations were assessed by randomly selecting tomato plants in a zigzag pattern across each field. From 10 randomly chosen plants per field, adult whiteflies were counted on the top, middle and bottom leaves during the morning hours, when insect activity was minimal (35). The percent disease incidence was calculated using the following formula (36):

$$\text{Percent disease incidence} = \frac{\text{Number of infected plants}}{\text{Total number of plants observed}} \times 100$$

Molecular characterization of MYMV in field-collected samples of blackgram

DNA isolation

DNA was extracted from two representative leaf samples per location. Total DNA was extracted from virus infected samples using the GEM-CTAB protocol (26). The DNA was stored at –20 °C for further use.

Detection and confirmation of the virus through PCR

PCR analysis was performed using DNA extracted from YMD infected blackgram samples. Initially, a degenerate primer pair was used to confirm the presence of begomoviruses (~1.2 kb) (37). Subsequently, to confirm mungbean yellow mosaic virus (MYMV), PCR was carried out using three pairs of MYMV-specific primers viz. MYMV DNA-A CP (specific for the AV1 region), MYMV DNA-B MP (specific for the movement protein) and MYMV DNA-A replication associated protein (REP-specific for AC1) (Table 1). The PCR reaction was carried out with a reaction mixture of 25 µL which included 12.5 µL of 2 X Genei master mix (readymade mix of Taq polymerase, dNTPs and PCR buffer, Genei Laboratories Pvt. Ltd., cat no # 0667700041730), 5 µL of template DNA and 2 µL of both forward and reverse primers (10 pm/µL). The volume was adjusted to 25 µL with sterile distilled water. PCR conditions included an initial denaturation at 94 °C for 2 min, followed by 30 cycles of denaturation at 94 °C for 50 sec, annealing at 52 °C for 45 sec, extension at 72 °C for 1.30 min and final extension at 72 °C for 15 min.

The PCR products were visualized on 1 % agarose gel electrophoresis and molecular markers such as 100 bp and 1 kb ladders were used to confirm the amplicon sizes of the target fragment. Further, one PCR-positive sample from Vellimalaipattinam (VMP) representing coat protein (VMP-CP) and two samples from AC and RI, Kudumiyanmalai (KDM), representing both movement protein (KDM-MP) and replication protein (KDM-REP), were selected for sequencing to further confirm the virus identity. They were sequenced at Biokart Pvt. Ltd., Bengaluru. The sequence data were assembled using Bioedit 2.0 and analyzed through a BLAST search in the NCBI databases (https://www.ncbi.nlm.nih.gov). The assembled sequences were submitted to the NCBI database and the accession numbers were obtained.

Whitefly transmission

Transmission studies of MYMV by *B. tabaci* using different acquisition access periods

For the whitefly mediated transmission of MYMV, a pure culture of *B. tabaci* Asia I cryptic species (OR646642), maintained on brinjal plants in insect-proof cages under controlled conditions was used. Whiteflies were allowed to acquire the virus from MYMV-infected blackgram plants, which were confirmed through PCR using CP-specific primers. Different AAPs of 15 min, 30 min, 1 hr, 3 hr, 6 hr, 12 hr and 24 hr were tested. Each AAP treatment was replicated three times, with four plants per replication and one clip cage with twenty whiteflies per plant was used. For each AAP treatment, 20 whiteflies were released onto symptomatic plants and allowed to feed for the specified duration. After the acquisition periods, the twenty viruliferous whiteflies in clip cages were transferred to healthy blackgram seedlings of susceptible variety CO5 (10-12 days old). Irrespective of the AAP, a constant IAP of 24 hr was maintained for all treatments. Following the IAP, whiteflies were killed by spraying systemic insecticide (Imidacloprid 200SL at 0.4 mL/L). The inoculated seedlings were maintained in insect-proof conditions and symptom development was monitored for 21 days post inoculation. Virus transmission efficiency was assessed based on symptom expression and the presence of MYMV was further confirmed through PCR analysis using MYMV *CP* gene. Four replications were maintained, with four plants per replication.

Transmission studies of MYMV by *B. tabaci* using different inoculation access periods

In order to standardize IAP, 20 adult whiteflies were allowed to feed on MYMV infected blackgram plants exhibiting typical symptoms in clip cages for a fixed AAP of 24 hr, which was optimized in the previous experiment conducted. After acquiring the virus, the viruliferous whiteflies were transferred to 10 day-old healthy CO 5 blackgram seedlings to study the transmission efficiency at varying IAP. The whiteflies were allowed to feed on the healthy plants for different inoculation access periods of 15 min, 30 min, 1 hr, 3 hr, 6 hr, 12 hr and 24 hr. Four replications were maintained, with four plants per replication. Whiteflies were confined to individual plants using clip cages to prevent external movement. In both the transmission study experiments, following the inoculation period, the whiteflies were killed by spraying systemic insecticide (Imidacloprid 200SL at 0.4 mL/L) to prevent post treatment feeding.

The inoculated plants were maintained in an insect proof chamber and observed for symptom development for up to three weeks. The transmission efficiency (disease incidence) was calculated based on the number of plants exhibiting visible symptoms, while the presence of MYMV was further confirmed through PCR analysis using the MYMV *CP* gene.

Seed transmission

Seed transmission of MYMV: Grow-out test using infected plant seeds

To examine the role of seed in transmission of MYMV, a total of 100 seeds were collected from MYMV-infected CO 5 plants in the field at AC and RI, Kudumiyanmalai. The seeds were then thoroughly surface-sterilized using 1 % Teepol solution to eliminate external contaminants. After sterilization, the seeds were sown in pots with sterilized potting mixture (soil: sand: FYM in a 2:1:1 ratio). The pots were maintained in insect-proof chambers with 25 ± 2 °C, 65 ± 5 % RH, 16 hr light/8 hr dark photoperiod to prevent vector-mediated transmission.

Plants were monitored regularly up to 60 days after sowing (DAS) for any symptom expression and the leaf samples were collected from all 100 plants and subjected to molecular confirmation through PCR using the MYMV CP primers. In all the experiments, PCR negative leaf samples served as negative controls.

Table 1. Primers used in this study

Primer ID	Primer sequence (5' - 3')	Region amplified (start to end nt)	PCR amplicon size (bp)	Components detected	Source of primer
PARIv772	GGNAARATHTGGATGGA	772 to 1960 nt	1100	DNA-A	(38)
PALIC1960	ACNGGNAARACNATGTGGGC				
MYMV- DNA-A CPF	ATGGG(T/G)TCCGTTGTATGCTTG	182 to 1185 nt	1000	DNA-A Coat protein (CP)	(39)
MYMV - DNA-A-CPR	GGCGTCATTAGCATAGGCAAT				
MYMV-Rep FP	GCAAGCTTGCTTCCCGTACTTGACG	1744 to 2251 nt	500	DNA-A Rep protein (REP)	(40)
MYMV-Rep RP	TCTCTAGAGATCAGCTAGAGGAGG				
MYMV- DNA-B MPF	ATGGAGAATTATTCAGGCGCA	1219 to 2118 nt	980	DNA-B Movement protein (MP)	(39)
MYMV- DNA-B MPR	TTACAACGCTTTGTTCACATT				

Testing potential seed transmission of MYMV to next generation plants

Twenty-five seeds of the blackgram variety CO 5, harvested randomly from grow-out test plants, were thoroughly surface-sterilized using 1 % Teepol solution to eliminate external contaminants. The seeds were then placed on moistened blotter paper in sterile Petri dishes for 12 hr to soften the seed coat and facilitate dissection. Each seed was carefully dissected into three components viz. embryonic axis, endosperm and seed coat.

To ensure sufficient DNA yield and to minimize variability among individual seeds, tissues from five seeds were pooled together to constitute one biological replicate, resulting in five pooled samples per tissue type. In total, five biological replicates were tested for each seed component. Seeds from PCR-negative grow-out plants served as negative controls. DNA was extracted from each pooled seed part using the optimized CTAB protocol and analysed through PCR using MYMV CP primers to confirm the presence of the virus. In parallel, another set of 25 surface-sterilized seeds was used for a grow-out test to examine seed transmission of MYMV into second-generation plants. Plants were observed throughout their growth to assess the transmission efficiency.

Results

Disease incidence of MYMV in blackgram cultivars across selected districts of Tamil Nadu

In all five different locations of Tamil Nadu, various types of symptoms, such as mild and severe mosaic, mosaic mottling, intense yellow patches on leaves and pod discoloration were observed (Fig. 1). At each location, disease incidence was assessed from a sample of 100 plants. The highest percent disease incidence (PDI) of 78 % was recorded in Narasipuram of Coimbatore district in local cultivars during the vegetative and flowering stages. This was followed by Vellimalaipattinam, Coimbatore (PDI of 74 %), where severe mosaic symptoms were observed in local cultivars at the vegetative stage. Next, AC and RI, Coimbatore showed 72 % PDI in VBN 10 variety and 65 % PDI was observed at AC and RI, Kudumiyanmalai in CO 5 cultivar. The lowest disease incidence of 45 % was recorded in Sukkampatti of Madurai district in the local cultivar (Fig S1 ;Table S1).

Detection of begomovirus using Rojas and MYMV-specific primers

The presence of the begomovirus was confirmed through PCR using Rojas's primers and the expected amplicon of ~ 1.2 kb was obtained in all the ten representative samples from five locations tested, confirming begomovirus infection in the field samples (Fig. S2 a).

Further the samples were tested for MYMV using three specific primer pairs viz. MYMV DNA-A *CP*, MYMV DNA-B *MP* and MYMV DNA-A *REP*. The expected amplicon sizes ~1.0 kb for DNA-A CP, 980 bp for DNA-B *MP* and 560 bp for DNA-A *REP* were obtained in all the samples tested, which confirmed the presence of MYMV in the field collected samples (Fig. S2 b-d).

As a representative, PCR-positive samples from Vellimalaipattinam (VMP-*CP*) and samples from AC and RI, Kudumiyanmalai (KDM- *MP* and KDM *REP*), were further sequenced to identify the virus. The obtained nucleotide sequences were analyzed using the BLAST program (www.ncbi.nlm.nih.gov). The VMP-CP from Vellimalaipattinam showed 100 % identity, 0.0 E Value and 100 % query coverage with MYMV DNA-A sequences viz. PP539000, MN602422 and PP898172. KDM-REP from Kudumiyanmalai sequences showed 94.97 % identity, 0.0 E value and 100 % query coverage with MYMV DNA-B Tirupati segment (GenBank accession No. OR344932) and 94 % identity, 0.0 E value and 100 % query coverage with the MYMV East Godavari segment (OP432258) respectively. The DNA-B *MP* sequence showed 99 % identity, 0.0 E value and 100 % query coverage with MYMV DNA-B Hisar isolate (MW736041). The sequences of isolates were submitted in the GenBank database and they are available under accession numbers PQ384577 (VMP-CP), PV500803 (KDM-MP) and PV500802 (KDM-REP).

Transmission of MYMV by the vector whitefly

Effect of different acquisition access periods (AAP)

Transmission efficiency of MYMV by *B. tabaci* increased with longer AAP. No transmission occurred at 15 min, 30 min or 1 hr AAP, as confirmed by symptom observation and PCR analysis. A minimum AAP of 6 hr was required for successful transmission, with 25 % of plants developing mosaic symptoms by 24 DAT. Transmission efficiency rose markedly with 12 hr AAP (75 %, symptoms at 18 DAT) and reached 87.5 % at 24 hr AAP, where plants showed severe mosaic, curling and stunting as early as 12 DAT (Table 2; Fig. 2a-g, 3). Based on these findings, 24 hr AAP was selected for further experiments due to its high and consistent transmission efficiency.

Effect of different inoculation access periods (IAP)

Similar to AAP, IAP enhanced MYMV transmission efficiency. No transmission occurred at 15 min, 30 min or 1 hr IAP. A 6 hr IAP resulted in 56.3 % infection, with symptom expression around 22 DAT. Efficiency further increased to 87.5 % at 12 hr IAP, with earlier symptom appearance (19 DAT). The highest efficiency was obtained at 24 hr IAP (93.8 %), where 15 out of 16 plants showed typical MYMV symptoms as early as 12 DAT, confirmed by PCR amplification of the *CP* gene (Table 3; Fig. 4a-g, 5).

In summary, both AAP and IAP showed a clear positive correlation between exposure time and MYMV transmission efficiency, with maximum infection achieved at 24 hr IAP. Symptom onset was earlier and more severe with longer exposure times.

Confirmation of seed transmission nature of MYMV through grow out test

Seeds collected from MYMV infected CO 5 plants from the field at Kudumiyanmalai, Pudukottai district were used for a grow-out test. Plants raised from these seeds remained symptomless even up to seed setting stage, showing no typical MYMV symptoms such as yellow mosaic patterns, leaf curling or stunted growth. However, molecular analysis revealed contrasting results. A total of 100 leaf samples from the blackgram variety CO 5 (SC) were subjected to PCR using primers specific for MYMV coat protein (CP) gene. The results showed that out of 100 samples tested, 51 samples were positive for MYMV CP. These findings suggested that seed transmission efficiency was 51 %, but all are asymptomatic (Fig. 6, 7). Although all grow-out plants were symptomless, PCR confirmed 51 % were MYMV-positive.

To investigate the seed transmission nature of MYMV, seeds were collected from grow-out test plants categorized into malformed and healthy seeds. Each seed was dissected into

Table 2. Transmission efficiency of MYMV by *B. tabaci* under different acquisition access period (AAPs) in blackgram

S.No.	Acquisition access period (AAP)	Inoculation access period (IAP)	No. of plants expressed symptom / Total no. of plants	Transmission efficiency*	Days taken to express symptom
1.	15 min		0/16	0.00^{d} (0.71)	-
2.	30 min		0/16	0.00^{d} (0.71)	-
3.	1 hr		0/16	0.00^{d} (0.71)	-
4.	3 hr	24 hr	0/16	0.00^{d} (0.71)	-
5.	6 hr		4/16	25.00^{c} (5.05)	24
6.	12 hr		12/16	75.00^{b} (8.69)	18
7.	24 hr		14/16	87.50^{a} (9.38)	12
	SE (d)		-	0.17	-
	CD (0.05)		-	0.33	-

Table 3. Effect of different inoculation access periods (IAPs) on MYMV transmission by *B. tabaci* in blackgram

S.No	Inoculation access period (IAP)	Acquisition access period (IAP)	No. of plants expressed symptom / Total no. of plants	Transmission efficiency*	Days taken to express symptom
1.	15 min		0/16	0.00^{d} (0.71)	-
2.	30 min		0/16	0.00^{d}(0.71)	-
3.	1 hr		0/16	0.00^{d} (0.71)	-
4.	3 hr	24 hr	0/16	0.00^{d} (0.71)	-
5.	6 hr		9/16	56.25^{c} (7.53)	22
6.	12 hr		14/16	87.50^{b} (9.38)	19
7.	24 hr		15/16	93.75^{a} (9.71)	12
	SE (d)		-	1.543	-
	CD (0.05)		-	3.086	-

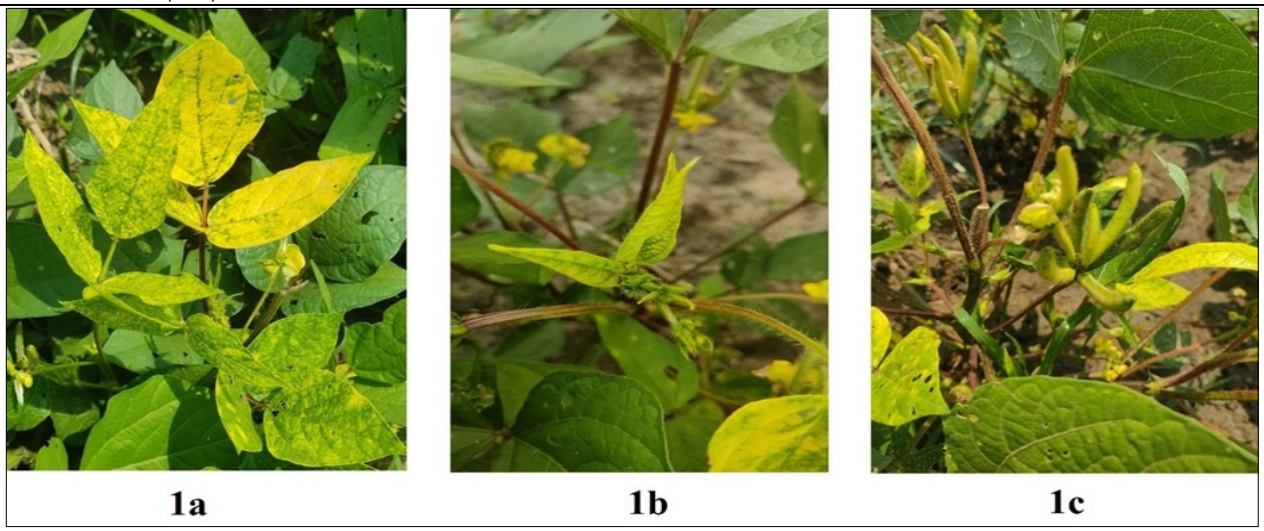

Fig. 1. Blackgram plants showing symptoms of yellow mosaic disease **(a)** yellow mosaic on leaves, **(b)** yellow specks in newly emerged leaves and **(c)** yellow discolouration in pod.

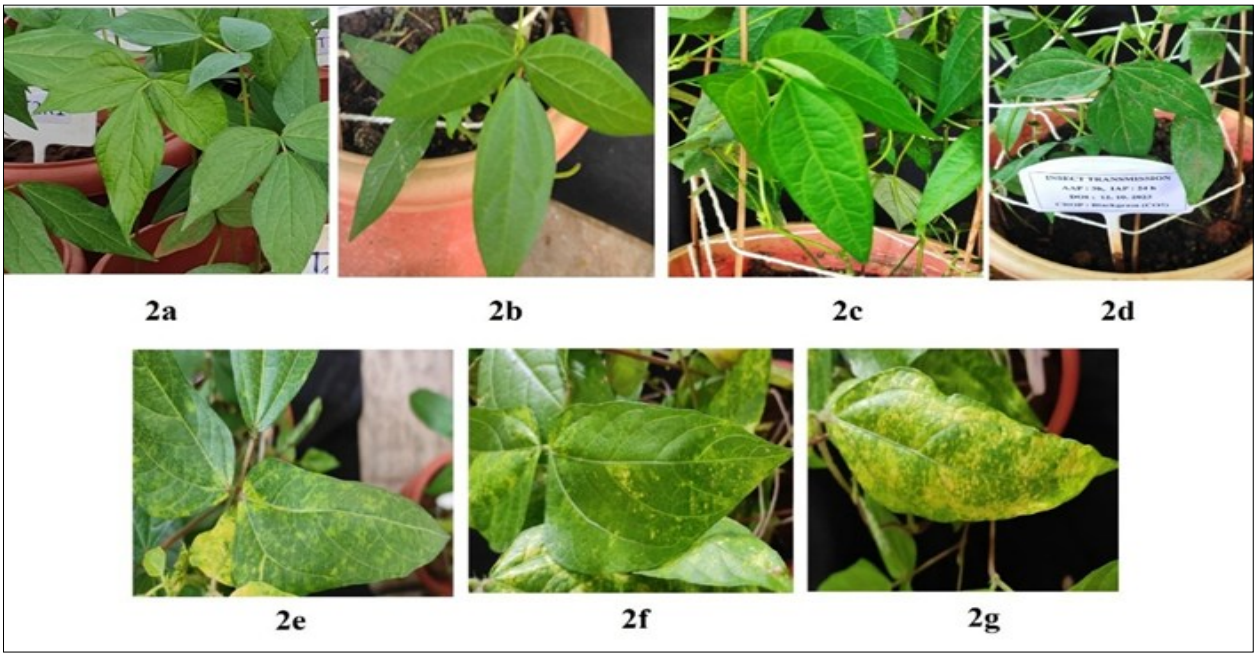

Fig. 2. Symptoms expressed upon different AAP treatments - Cultivar: CO Bg (5). **(a)** 15 min AAP and 24hr IAP; **(b)** 30 min AAP and 24hr IAP; **(c)** 1 h AAP and 24 hr IAP; **(d)** 3 h AAP and 24 hr IAP; **(e)** 6 h AAP and 24 hr IAP; **(f)** 12h AAP and 24 hr IAP and **(g)** 24 hr AAP and 24 hr IAP.

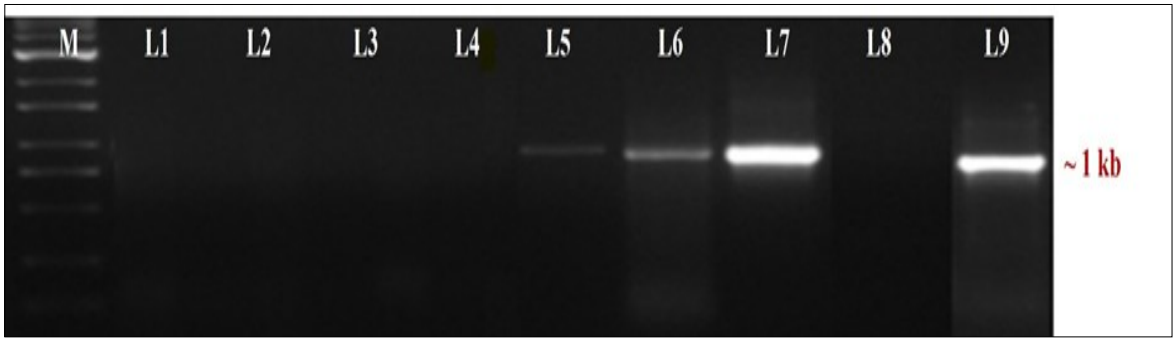

Fig. 3. Detection of MYMV in blackgram after whitefly transmission with different acquisition access period (AAP). M- 1 Kb ladder; L1- 15 min; L2 -30 min; L3 -1 hr; L4 -3hr; L5 -6hr; L6- 12hr; L7- 24 hr; L8 -negative control ; L9 -positive control (MYMV).

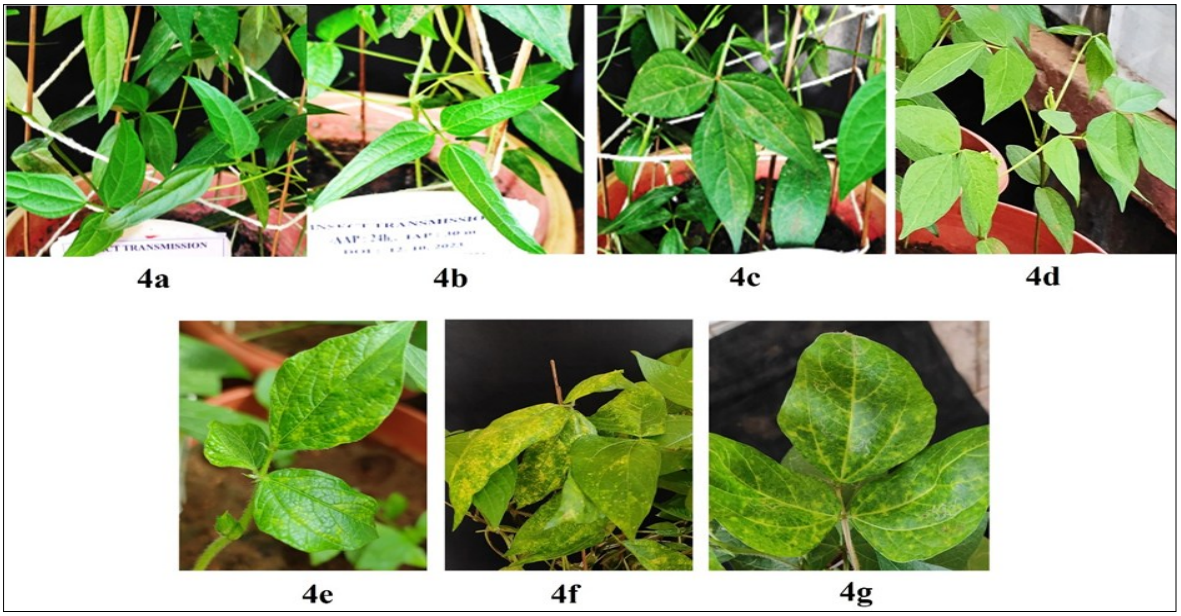

Fig. 4. Symptoms expressed upon different 1AP treatments - cultivar: CO Bg (5). **(a)** 15 min IAP and 24 hr AAP; **(b)** 30 min IAP and 24 hr AAP; **(c)** 1 h IAP and 24 hr AAP; **(d)** 3 hr IAP and 24 hr AAP; **(e)** 6 hr IAP and 24 hr AAP; **(f)** 12hr IAP and 24 hr AAP and **(g)** 24 hr IAP and 24 hr AAP.

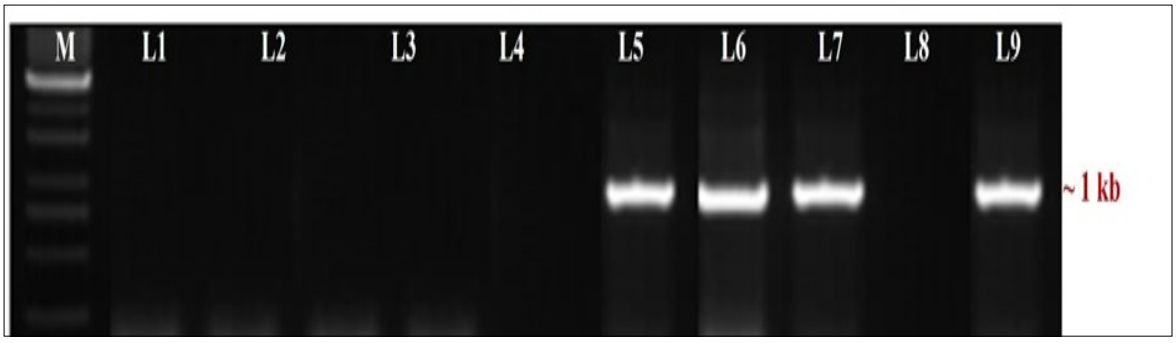

Fig. 5. Detection of MYMV in blackgram after whitefly transmission with different inoculation access period (IAP). M- 1 Kb ladder; L1- 15 min; L2 -30 min; L3 -1 hr; L4 -3hr; L5 -6hr; L6- 12hr; L7- 24 hr; L8 -negative control ; L9 - positive control min (MYMV).

Fig. 6. Grow-out test study of CO 5 seeds under insect proof cage in the glasshouse.

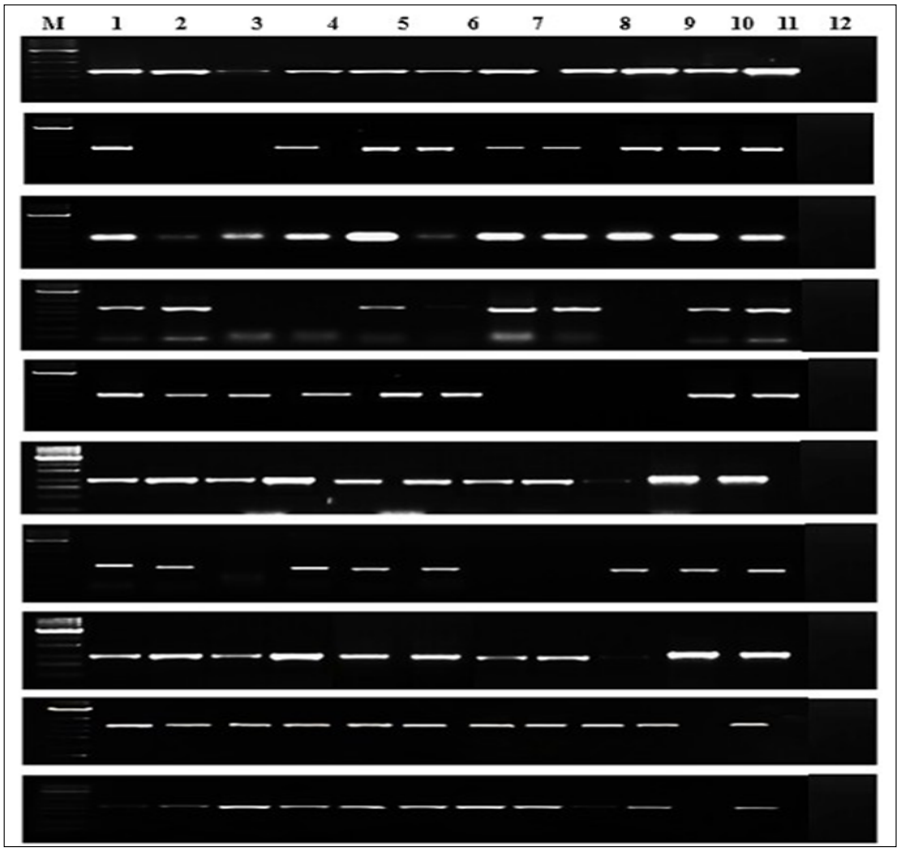

Fig. 7. Agarose gel electrophoresis of PCR amplicon of coat protein (*CP*) gene from grow out test plant CO5 (*SC*) of blackgram. Lane M -1 Kb ladder; L1 -10 -leaf samples collected from (100 grow out test plant leaf samples); L11 -positive control; L12 - negative control in each gel.

three components viz., seed coat, endosperm and embryonic axis, each was analysed through PCR. PCR results confirmed the presence of MYMV in all the three seed parts. In the case of endosperm and embryonic axis, four out of five samples were PCR positive for MYMV CP, whereas in seed coat all five samples were PCR positive (Fig 8a-e, 9), (Fig. S3a, b). The seeds from PCR negative grow-out test plants again tested negative in PCR. In the next generation plants grown from seeds collected from first generation grow out plants, ten out of 25 plants (40 %) were PCR positive, indicating carryover of MYMV to next generations. However, all plants remained asymptomatic, likely due to diffused light inside the insect-proof cage, which supressed symptom expression. These results indicated that the light intensity may play crucial role in symptom proliferation (Fig. 10).

Discussion

Mungbean yellow mosaic virus (MYMV), a bipartite begomovirus, is a major constraint in blackgram (*V. mungo*) production, primarily transmitted by the whitefly (*B. tabaci)*, an efficient and widely distributed vector across South Asia. Traditionally, the epidemiology of begomoviruses has focused on vector-mediated transmission; however, recent studies have highlighted the complex and highly adaptable nature of *B. tabaci* in acquiring and transmitting MYMV, even under limited exposure times (39).

Seed transmission of plant viruses is a well-documented route of vertical dissemination and persistence in the agroecosystem. While begomoviruses were historically believed to lack seed transmission potential due to their phloem-limited nature and dependence on whitefly vectors (*B. tabaci*) for horizontal spread, emerging evidence has challenged this long-held paradigm. Among these, MYMV causing severe YMD in *Vigna* spp., has gained prominence due to its dual transmission routes, vector-mediated and seed-mediated. MYMV presence in various seed tissues, including the embryonic axis and established seed-to -seedling transmission in susceptible cultivars such as CO 5 (27, 40).

Epidemiology and incidence

The present study revealed a high prevalence of YMD in blackgram cultivars across selected districts of Tamil Nadu, with disease incidence ranging from 45 % to 78 %, underscoring the widespread infection by MYMV. The highest PDI was observed in local cultivars at Narasipuram (78 %), followed by Vellimalaipattinam (74 %) and VBN 10 at AC and RI, Coimbatore (72 %). The severity and distribution of YMD are influenced by the interaction of host susceptibility, vector population dynamics and environmental inoculum pressure (41). Similar spatial variability was reported, where the highest incidence (87 %) occurred during summer at Panpozhi, with considerable variation across Vamban and Coimbatore (24). Interestingly, while Coimbatore data showed a strong correlation between whitefly population and YMD incidence, no such association was evident at Vamban, highlighting that vector numbers alone may not directly predict disease outbreaks. No direct relationship between whitefly density and cotton leaf curl disease incidence, likely due to differences in viruliferous potential within whitefly populations, a factor also emphasized (24, 42). In addition, factors such as continuous cultivation of susceptible varieties, absence of crop rotation and favourable environmental conditions for whitefly multiplication may have contributed to the higher disease levels recorded in some areas of Tamil Nadu (43).

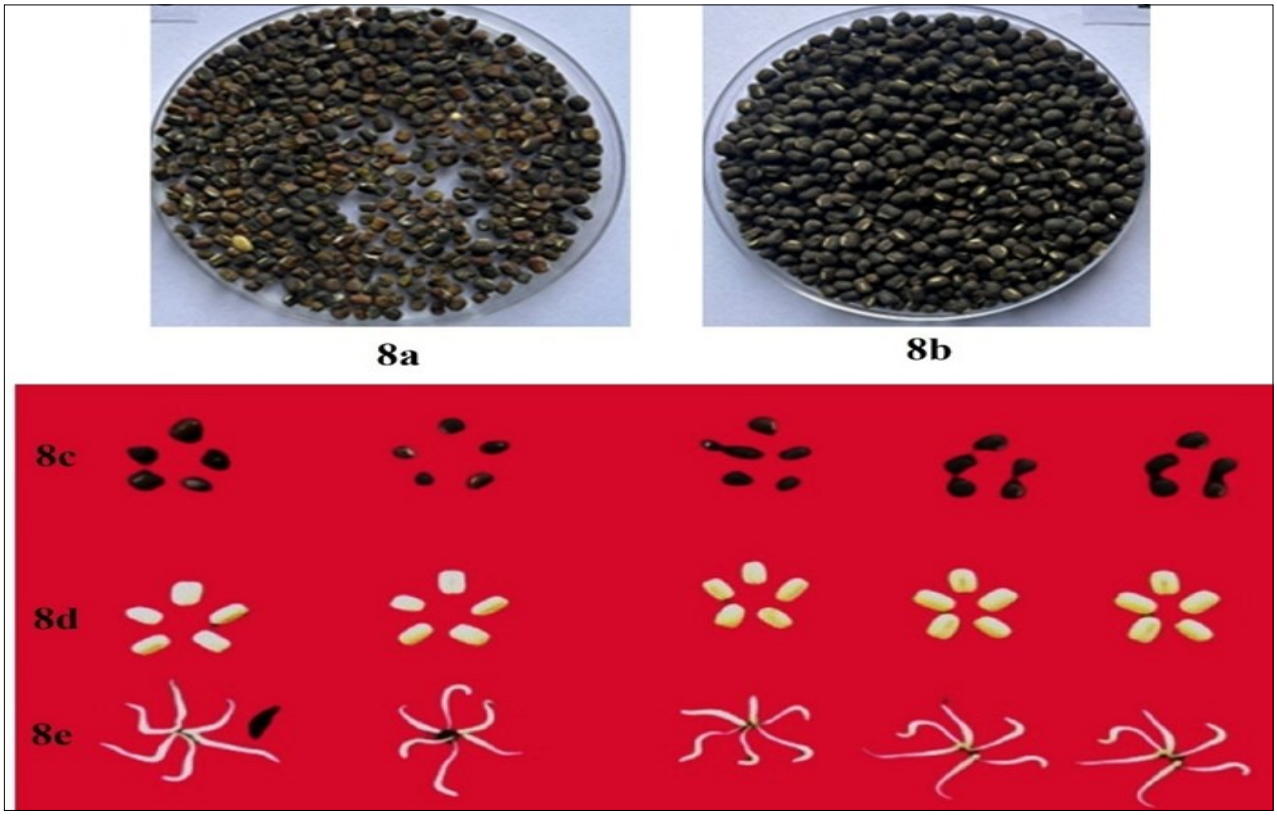

Fig. 8. Different part of seeds dissected for PCR analysis. **(a)** malformed seeds, **(b)** healthy seeds, **(c)** seed coat, **(d)** cotyledon and **(e)** embryonic axis.

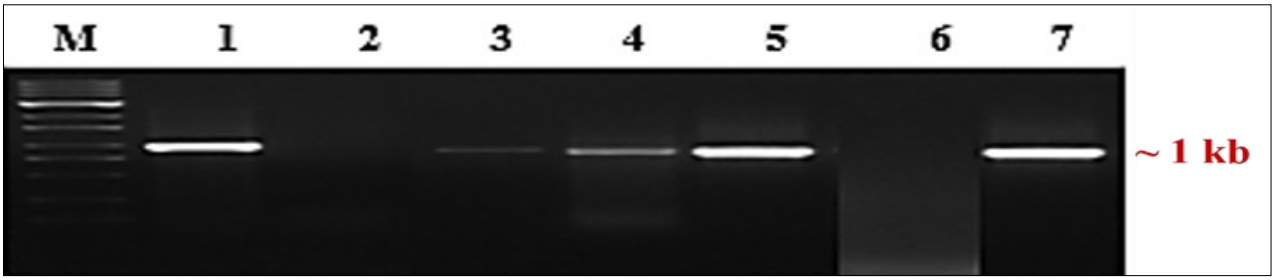

Fig. 9. Detection of MYMV in embryonic axes of CO5 seed.

Lane M -1 Kb ladder; L1 -5 – embryonic axes of seed samples collected from grow out test plants; L6 - negative control; L7 – positive control.

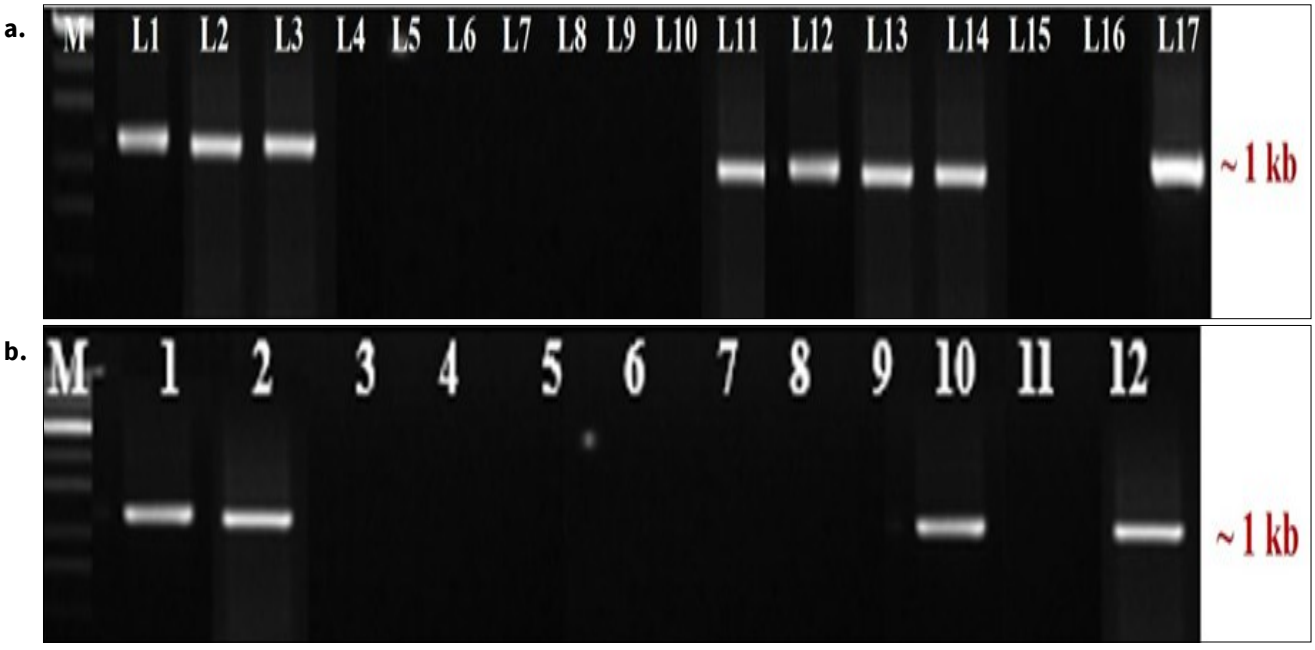

Fig. 10. Agarose gel electrophoresis of PCR amplicon of coat protein (CP) gene from grow out test plant CO5 (SC) of blackgram - Second generation. a) Lane M -1 Kb ladder; L1 -15 - seed samples collected from second generation grow out test plants; L16 - Negative control; L17 - positive control. b) Lane M -1 Kb ladder; L1 -10 - seed samples collected from grow out test plants- second generation; L11 - negative control; L12 – positive control.

Molecular detection and sequence diversity

PCR assays with CP, MP and REP primers confirmed MYMV in all samples, consistent with earlier reports on PCR reliability for begomovirus detection in leguminous hosts (34, 40, 44). Further molecular characterization through nucleotide sequencing of PCR-positive samples from Vellimalaipattinam (VMP-CP) and Kudumiyanmalai (KDM-MP and KDM-REP) revealed high sequence identity with previously reported MYMV isolates.

Moreover, the observed sequence similarities with isolates from geographically distant regions such as Karnataka, Punjab and Andhra Pradesh indicated a degree of genetic conservation and regional adaptation among MYMV strains. This is consistent with earlier reports, which highlighted the genetic diversity and molecular variability of MYMV across India (44, 45).

Vector transmission (IAP/ AAP)

In the present study, transmission efficiency increased with longer feeding periods, confirming the role of AAP/IAP in virus acquisition and inoculation. The findings revealed a positive correlation between the duration of AAP/IAP and MYMV transmission, both in terms of symptom expression and molecular confirmation through PCR.

Our study demonstrated that very short AAPs of up to 1 hr were insufficient for MYMV transmission, as no symptoms or PCR -positive plants were detected. This finding indicates that the virus requires a minimum feeding duration for efficient acquisition, consistent with earlier reports on begomoviruses, where negligible transmission was observed at brief AAPs and efficiency increased substantially only after longer feeding periods (46, 47)). Although, MYMV could be transmitted with just 15 min of acquisition in green gram, the efficiency was minimal, supporting our observation that at least 6 hr is required for reliable transmission (48). Transmission efficiency rose sharply with extended AAPs, reaching near-complete levels at 12–24 hr. Similar patterns have been described in mungbean and with different biotypes of *B. tabaci*, reinforcing the importance of prolonged acquisition for successful inoculation and symptom development (46, 49).

Comparable trends were observed in IAPs. Short feeding durations failed to result in infection, whereas efficiency increased significantly beyond 6 hr and peaked at 24 hr. This is in agreement with previous studies demonstrating that longer inoculation periods greatly enhance transmission of MYMV and related begomoviruses (46, 50). Furthermore, transmission efficiency is strongly influenced by vector density (51, 52). In line with these studies, our use of 20 viruliferous whiteflies per plant ensured high and consistent infection rates.

At shorter AAPs (≤1–6 hr), symptom expression was delayed compared to longer AAPs. This can be attributed to insufficient virus acquisition by whiteflies, resulting in lower initial viral load delivered to plants during inoculation. A smaller inoculum likely requires additional replication cycles within host cells before reaching the threshold needed to trigger visible symptoms, thereby extending the latent period between inoculation and symptom expression. Such latent period effects have been noted in begomoviruses, where both the quantity of virions ingested and the efficiency of their delivery influence the timing and severity of symptom development (46, 47).

Seed transmission

The present investigation provided strong evidence that MYMV is seed-transmitted in blackgram cultivar CO 5. A grow-out test conducted with seeds collected from symptomatic YMD infected plants from Kudumiyanmalai (Pudukottai district) resulted in blackgram seedlings with no visible signs of yellow mosaic, leaf curling or stunting. However, molecular diagnostics using MYMV coat protein (*CP*) gene specific primers revealed 51 % PCR-positivity, indicating a high proportion of asymptomatic infections. These findings align with the concept of latent or cryptic viral infections, where viral replication occurs without overt symptom expression. These results resonate with findings, which reported the presence of MYMV in whole seeds, seed coats, cotyledons and embryonic axis of blackgram cv. CO 5 using multiple detection methods (PCR, ELISA, ISEMand southern hybridization) and confirmed 32 % seed-to-seedling transmission, although seedlings remained symptomless (24). The detection of MYMV in the embryonic axis in both studies suggests a vertical transmission pathway.

Interestingly, the genotype-dependent seed transmission of MYMV, where susceptible cultivar CO 5 harboured the virus in all seed parts including embryonic axis, while resistant cultivar Mash 114 lacked the virus in the embryonic axis, despite detection in seed coat and cotyledon (40). This genotype-linked viral exclusion from the embryo provides a plausible mechanism for the variability in seed transmissibility across cultivars.

In contrast, MYMV detected in reproductive tissues and seeds of mungbean (*V. radiata* cv. GM-4), but not in embryonic axes and reported PCR-negative seedlings (53). However, MYMV was seed-borne but not truly seed-transmitted, highlighting potential host or genotype-specific restrictions in virus movement within the seed.

Comparisons with other begomoviruses

Our findings are comparable to the seed transmission behaviour of other bipartite begomoviruses. Bitter gourd yellow mosaic virus (BgYMV) showed true seed transmissibility, with the virus detected in various seed parts including embryos and a 32.05 % seed to seedling transmission (31). Similarly, Dolichos yellow mosaic virus (DoYMV) was found in seed components and progeny seedlings, although the latter often lacked symptoms, mirroring the latent infection pattern observed in the present study (30). The transmission dynamics, localization and titre of tomato leaf curl New Delhi virus (ToLCNDV) in bitter gourd, ridge gourd and pumpkin (54). Transmission of ToLCNDV was found to be 80 % efficient at AAP and IAP of 24 hr.

Similar observations found in a grow-out tests in insect-proof cages using three bitter gourd hybrids (H1, H2 and H3) and viral presence was detected through PCR using BgYMV and ToLCNDV-specific primers (32). While no seed transmission was recorded for BgYMV, ToLCNDV was transmitted in 5 % of H1 and H2 plants and 3 % of H3 plants. In a microplot experiment using a different seed lot of H1 hybrids, a higher seed transmission rate of 43.2 % was observed. Among these, 4.8 % of plants displayed mild mosaic and mottling symptoms, whereas 38.4 % remained asymptomatic yet tested positive for ToLCNDV, highlighting the potential for latent infections in progeny seedlings.

From a broader perspective, studies on other begomoviruses, like pepper yellow leaf curl Indonesia virus (PepYLCIV) and tomato yellow leaf curl virus (TYLCV), confirmed not only seed-to-seedling transmission but also systemic movement and whitefly acquisition from symptomless infected progeny (55, 56). In contrast, Bhendi yellow vein mosaic virus (BYVMV), though present in reproductive tissues and seed parts, failed to transmit to seedlings, emphasizing that seed-borne status does not necessarily equate to seed transmissibility (57).

The seed transmissibility of Okra enation leaf curl virus (OELCuV) in bhendi hybrids, confirming its presence in asymptomatic seedlings through ELISA and PCR (58). Moreover, 21.7 % and 4 % of seedlings from H1 and H2 hybrids, respectively, tested positive for OELCuV, indicating genotype-dependent variation in seed transmission efficiency. Similarly, no transmission was observed in Bhendi yellow vein mosaic virus (BYVMV), suggesting selective seed transmissibility among begomoviruses (46). The presence of OELCuV in dissected seed parts, including the seed coat, endosperm and embryo, validating its systemic movement and potential for vertical transmission (47).

Implications for management

In this study, the results provide robust evidence that MYMV is both vector-transmissible and seed-transmissible in blackgram cultivar CO 5, highlighting dual modes of virus perpetuation and spread. The vector transmission experiments demonstrated that a 24 hr AAP and IAP by *B. tabaci* resulted in the highest transmission efficiency, emphasizing the importance of exposure duration in virus acquisition and delivery. The successful detection of MYMV in symptomless seedlings and its localization within embryonic seed tissues, particularly the embryonic axis, confirmed true seed transmission and underscores the risk of latent infections acting as cryptic inoculum sources. This is the first study confirming seed transmission up to second-generation seedlings raised from first generation plant seeds. The asymptomatic young blackgram seedlings served as an inoculum source even when exposed to minimal whiteflies in the field, leading to rapid dissemination in a huge population of healthy plants in the same and adjacent fields. These findings are not only consistent with previous reports on MYMV and related begomoviruses but also reinforce the need for integrated disease management strategies. In particular, early-stage vector control and routine molecular diagnostics in seed certification programs are crucial to prevent both horizontal and vertical spread of MYMV. Collectively, the dual transmission potential of MYMV poses significant epidemiological and phytosanitary challenges, necessitating vigilant monitoring, improved seed health testing and targeted vector management to safeguard blackgram cultivation in endemic regions.

Conclusion

The present investigation establishes that MYMV is seed-transmissible in blackgram, with latent and asymptomatic infections serving as hidden inoculum sources that complicate virus-free seed production and enhance the risk of long-distance spread through seed trade. In addition, transmission assays confirmed that MYMV spread by the whitefly vector *B. tabaci* is highly dependent on acquisition and inoculation access periods, with 24 hr exposures resulting in the highest transmission efficiency. These results highlight the dual epidemiological threat of MYMV through both vertical (seed-mediated) and horizontal (vector-mediated) pathways.

To mitigate this risk, the integration of molecular diagnostics in seed health certification, combined with early and targeted vector management, is crucial to restrict primary infections and subsequent field-level outbreaks. Furthermore, the findings underscore the importance of resistance breeding and phytosanitary measures to support sustainable blackgram production and safeguard seed systems against the long-distance dissemination of MYMV.

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Authors' contributions

SR contributed to the original draft writing, conducted the experimental work and validated the results. NS and RP were responsible for conceptualization, methodology, supervision and critically revising the manuscript draft. YI, RJ, YA and VS were involved in revising the draft, including the incorporation of tables and figures and proofreading. All authors have read and approved the final version of the manuscript.

Compliance with ethical standards

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

Ethical issues: None

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