



Aleurothrixus trachoides (Back) can transmit begomovirus from *Duranta* to potato, tomato and bell pepper

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Solanum whitefly, *Aleurothrixus trachoides* (Back). (Hemiptera: Aleyrodidae) was considered as a non-virus vector by European and Mediterranean Plant Protection Organization (EPPO) reports. However, in the present study it was found to transmit *Duranta leaf curl virus* (DLCV) to tomato, bell pepper and potato. *A. trachoides* infested field samples of *Duranta* sp (100%) and tomato (20%) tested positive for begomovirus by PCR using begomovirus degenerate primers and primers specific to *Tomato leaf curl New Delhi virus* showing amplicon of 520 bp and 2.7 Kb respectively. The DNA samples of *A. trachoides* collected from virus positive *duranta* and tomato plants also tested positive for the virus. Virulent whiteflies from *duranta* could successfully transmit DLCV to bell pepper (26%) and tomato (13%) plants as confirmed by Rolling Circle Amplification. The rate of virus transmission by *A. trachoides* from DLCV inoculated tomato to bell pepper and tomato to potato was 100% and tomato to tomato was 80%. The results suggest whitefly *A. trachoides* as the vector for DLCV and to the best of our knowledge, this is the first report for *A. trachoides* as vector of begomovirus. These findings suggest need for reconsideration of *A. trachoides* as a virus-vector. This will have great impact on solanaceous vegetable cultivation in India and other parts of the world.

Keywords. *Aleurothrixus trachoides*; *Duranta leaf curl virus*; *Duranta*; tomato; bell pepper; potato; begomovirus vector

1. Introduction

Solanum whitefly, *Aleurothrixus trachoides* (Back) (Hemiptera: Aleyrodidae) is an important insect pest mostly on plants species of the family Solanaceae and Convolvulaceae. *A. trachoides* reported to occur on plants such as tomato (*Solanum lycopersicum*), bell pepper (*Capsicum annuum*), eggplant (*Solanum melongena*) and tobacco (*Nicotiana* spp.), ornamental plants like *Duranta* spp and weeds such as *Solanum nigrum* and *Ipomoea* spp. According to European and Mediterranean Plant Protection Organization (EPPO) reports, *A. trachoides* is native to neo-tropics and recently reported to occur in Africa, North America, Central America, Caribbean, South America, Oceania

and Asia (EPPO 2017). In India, it was reported for the first time on *Duranta erecta* and *Capsicum annum* - from Karnataka (Dubey and Sundararaj 2015). Subsequently, whitefly has established on large number of plant species in Karnataka, Tamil Nadu, Kerala and Maharashtra states of India (Sundararaj *et al.* 2018).

The damage caused by *A. trachoides* reported to be due to direct feeding on plant sap and through the production of honeydew, which promotes the growth of sooty moulds. Until now, there are no reports of *A. trachoides* transmitting any plant virus. EPPO did not consider *A. trachoides* as a virus-vector (EPPO 2017). During our survey in Maharashtra, India, we frequently observed typical symptoms of begomovirus infection in the *A. trachoides* infested *duranta* and

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tomato plants. *Duranta leaf curl virus* (DLCV) has been reported on *duranta* from India in 2009 (Sharma et al. 2009). The sequence of DLCV shows similarity to *Papaya leaf crumple virus*-PLCV (98%), *Rose leaf curl virus* (92–95 %) and 87–89% similarly to *Tomato leaf curl virus* (Marwal et al. 2013). Recently begomovirus infecting *D. repens* was characterised, wherein the DNA-A component shows 92.2% similarity with *Catharanthus yellow mosaic virus* (CAYMV) and *Chilli leaf curl India virus* while DNA-B component has 95.2% similarity with *Tomato leaf curl New Delhi virus* – ToLCNDV (Anwar and Tahir 2018). Iram et al. (2004) observed that 407 nucleotides in the virion-sense of DLCV shows identity to *Croton yellow vein virus* and 462 nucleotides in the complementary-sense shows identity with PLCV, based on these findings DLCV was considered as a recombinant virus. There are no reports on the probable vector for the begomoviruses infecting *duranta*. The genus *Begomovirus* is the largest in the family Geminiviridae, with 288/325 species. Virus genome can be bipartite (DNA-A and DNA-B) or monopartite (resembling DNA-A). Begomoviruses cause significant economic losses worldwide especially in important vegetable crops such as tomato, peppers, cucumber, pumpkin, melon, eggplant etc. The losses due to begomoviruses were about 40–100% depending up on the stage of infection (Chakraborty et al. 2003). Whiteflies transmit about 140 viruses, mostly begomoviruses. Dominant vector species being *Bemisia tabaci*, which transmits 111 viruses, while *Trialeurodes vaporariorum* and *T. abutilonia* transmits three viruses each (Njoroge et al. 2017). The present study intended to identify the association of *A. trachoides* with begomoviruses.

2. Methodology

2.1 Collection of whitefly samples and identification

The samples of *A. trachoides* collected from different host plants (tomato, *duranta*, potato, peppers and weeds) in the Pune region of Maharashtra state, India and stored in 100% ethanol. For morphological identity, along with adult whiteflies, leaf samples containing nymphs and pupae were also collected. Morphological identity for most of the whitefly samples collected was provided by Dr. A.K. Dubey, Zoological Survey of India, Andaman & Nicobar Regional Centre Haddo, Port Blair.

2.2 Whitefly species determination by PCR

Total DNA extracted from individual whiteflies using DNAeasy Blood and Tissue Kit (Qiagen, Amph, Germany) by following manufacturer's protocol with slight modification. Insects were homogenised in micro-centrifuge tubes using hand homogenizer in 20 µl of ATL buffer and then added another 30 µl of ATL buffer, lysed at 56°C for 2 h. DNA eluted from the column in 30 µl of AE buffer.

The mitochondrial cytochrome oxidase 1 (mtCOI-I) region was amplified from genomic DNA of single whitefly using the primers LCOI490-F and HCO2198-R (Folmer et al. 1994). PCR was performed in 20 µl PCR mixture (10 µl of 2XPCR master Mix, 2 µl of genomic DNA/~ 50 ng/µl, 1 µl each of LCOI490 and HCO2198 and 6 µl of nuclease free water) (PCR conditions given in supplementary table 1).

2.3 Collection of plant samples and detection of begomoviruses

The *A. trachoides* infested plants showing typical symptoms of begomovirus infection were collected along with whiteflies and stored at –80°C. DNA was extracted from plant samples using DNAeasy Plant Kit (Qiagen, Amph, Germany) by following manufacturers protocol. Similarly, DNA was extracted from individual whitefly samples collected from each plant in triplicate. The extracted DNA samples stored in –20°C for further use. DNA extracted from same whiteflies sample was used both for biotype determination and virus detection. The genomic DNA of whitefly and plant samples were tested for begomovirus using degenerate primers (Deng et al. 1994) and ToLCNDV specific primers (Reddy et al. 2010).

PCR using degenerate primers Deng 540/Deng 541 was performed in 20 µl PCR mixtures (10 µl of 2X PCR master mix, 2 µl containing ~ 50 ng/µl of genomic DNA, 1 µl each of Deng540 and Deng 541 and 6 µl of nuclease free water). For PCR amplification of ToLCNDV, specific primers were used. The 20 µl PCR reaction mixture consisted of 10 µl of 2X PCR master mix, 2 µl of genomic DNA containing ~ 50 ng/µl, 1 µl each of forward and reverse primers and 6 µl of nuclease free water (supplementary table 1).

2.4 Virus transmission studies

2.4.1 *Transmission using A. trachoides from naturally infected duranta to tomato and bell pepper:* Three

weeks old seedlings of tomato and bell pepper maintained inside insect proof cages were given inoculation feeding with the virulent *A. trachoides* (25/ plant) collected from virus-infected duranta plants. Whiteflies were directly collected into 50 ml falcon tubes (the bottom of the tubes were fitted with insect proof net). Individual plants were covered with tubes containing virulent whiteflies, allowed to feed for 3 days, and then killed by applying insecticide (figure 1).

2.4.2 Virus transmission studies with *A. trachoides* from inoculated tomato to other hosts: *A. trachoides* cultured on healthy bell pepper plants were utilised for transmission studies. Absence of virus in whiteflies and host plants was confirmed by PCR using virus specific primers.

Healthy tomato inoculated with DLCV was utilised for further transmission to other healthy host plants. Virus infection was confirmed by Rolling Circle Amplification (RCA) with DNA extracted from DLCV inoculated tomato followed by restriction digestion with *Bam*HI. The 2.7 kb fragment of RCA digested product was gel-extracted and sequenced.

Transmission was carried out by following the artificial diet feeding method (Upadhyay *et al.* 2011) modified by Dixit *et al.* (2013). About 25 numbers of virus free *A. trachoides* cultured on bell pepper were fed for 48 h on leaf disc of virus positive tomato plants,

placed on solidified (1%) agar agar, in the inner side of the bioassay vial caps (figure 1). The whiteflies were then used for transmission to healthy tomato, potato and bell pepper plants (15 each) as described above. Transmission done with whiteflies similarly but fed on leaf discs of healthy tomato plant served as control.

The total DNA was isolated after six weeks of inoculation and used for virus detection by PCR using specific primers as described earlier. Primary PCR product was used as DNA template for secondary PCR whenever the primary PCR results are inconclusive due to faint bands on gel. Sequencing of 520 bp amplicons obtained from degenerate primers was done in triplicate for duranta, tomato, bell pepper, and whiteflies fed on virus positive tomato leaf discs.

2.5 Rolling Circle Amplification (RCA) and endonuclease restriction digestion

RCA was performed using TempliPhi™ kit (GE Healthcare, USA). 1 µl (100ng) of DNA was mixed with 5 µl of sample buffer (Provided in the kit) and denatured at 95°C for 3 min using thermal cyclers and chilled on ice for 10–15 min. Reaction buffer (5 µl) and enzyme mix provided in kit (0.2 µl, phi29 DNA polymerase) were added to the cooled tubes and incubated at 30°C for 18 h. The reaction terminated by heat treatment at 65°C for 10 min and stored at –20°C. The RCA product was digested over night with restriction endonuclease *Bam*HI in a 30 µl reaction mixture (5 µl of RCA product, 3 µl 10x buffer, 0.5 µl BSA and 21.5 µl water) at 37°C. Approximately 2.7 kb DNA band was separated on agarose gel and sequenced.

2.6 DNA extraction from gel

Required DNA bands from all the above PCR and digested RCA product separated on the gel were purified using QIAquick® gel extract kit (Qiagen, Amph, German) by following protocol provided in the kit.

2.7 Sequence and phylogenetic analysis of gene

DLCV sequences were assembled by using BioEdit software version 7.2 and compared with the previously reported sequences around the world (<http://www.ncbi.nlm.nih.gov/Genbank/index.html>). The sequences and

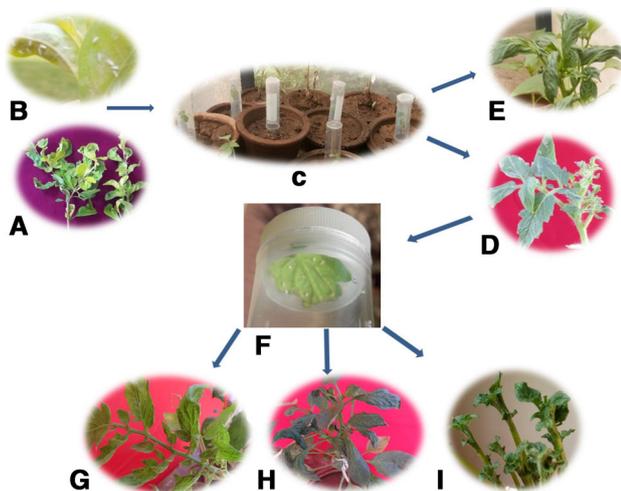


Figure 1. Duranta showing leaf curling (A) and *A. trachoides* (B); (C-F) schematic representation showing virus transmission by *A. trachoides* collected from virus-infected duranta to tomato (D) and bell pepper (E); (F-I) virus transmission using *A. trachoides* by leaf disc feeding method (F) from virus inoculated tomato to tomato (G), bell pepper (H) and potato (I).

their identity details are given in supplementary sequences and supplementary table 2–4.

Multiple sequence alignment and identity matrix performed for the nucleotides and amino acid sequences (using CLUSTAL-W and BioEdit v.7.2). Phylogenetic analysis was conducted using (MEGA version X) by the Neighbor-Joining method (Saitou and Nei, 1987) and the bootstrap test (1000 replicates) to construct phylogenetic tree (Felsenstein 1985) using an isolate of DLCV isolate 57SA segment DNA-A (NC_038980.1) as out-group. The evolutionary distances were computed using the p-distance method (Nei and Kumar, 2000; Kumar et al. 2016) and were in the units of the number of amino acid differences per site. The nucleotide sequences obtained from inoculated plants were compared for similarity with DLCV isolate 57SA segment DNA-A (NC_038980.1) and PLCV (HM140368.1).

2.8 Detection of β satellite in whitefly and plant samples

DNA isolated from plant and *A. trachoides* tested for the occurrence of β satellite using universal primers Beta 01 and Beta 02 (Bridson et al. 2003). The 25 μ l PCR reaction mixtures consisted 12.5 of 2X PCR master Mix, 1 μ l of genomic DNA (~ 50 ng/ μ l), 1 μ l each of forward and reverse primers and 9.5 μ l of nuclease free water (supplementary table 1).

3. Results

3.1 Sampling of whiteflies (*A. trachoides*) and its host plants for the occurrence of Begomovirus

3.1.1 Whitefly species identification and virus detection: Whitefly samples collected were identified morphologically as *A. trachoides* by Zoological Survey of India, Andaman & Nicobar Regional Centre Haddo, Port Blair. Further, PCR with DNA of whiteflies using mtCOI-I specific primers amplified ~ 658 bp DNA (Supplementary Figure 1). Analysis of amplicon sequences for the whiteflies collected from duranta, bell pepper and tomato showed 99.4–100% sequence similarity with *A. trachoides* (KP032218.1), thus confirming identity of whitefly samples (supplementary table 2).

3.1.2 Detection of virus in whitefly and plant samples: Virus affected duranta plants showed typical

symptoms of begomovirus infection such as severe stunting, apical leaf curling and leaf crinkling. Similarly, virus-infected tomato showed symptoms like crinkling, slight upward and downward curling, veinal enation, leathery leaf, chlorosis, yellowing and stunting. Diseased bell pepper showed symptoms like rugosity, mottling, vein banding, downward cupping, leathery leaf, veinal enation, dark green leaf and shortened internode. All duranta plant samples and 60% of *A. trachoides* collected from duranta tested positive for begomovirus. Only 2/10 *A. trachoides* infested tomato plants and 5/30 whitefly samples collected from tomato showed presence of virus. All the virus positive *A. trachoides* were from virus-infected plants. All the other hosts plants and *A. trachoides* on them tested negative for begomovirus (table 1).

3.2 Vector transmission

The virus transmission was done by using the *A. trachoides* collected from virus-infected natural host duranta to tomato and bell pepper. Whereas lab cultured virus free *A. trachoides* were utilised for transmission from virus-inoculated tomato to others host plants as shown in schematic diagram (figure 1)

3.2.1 Transmission by *A. trachoides* collected from virus-infected duranta plants: The PCR analysis results indicate that *A. trachoides* fed on virus-infected duranta plants successfully acquired virus (Figure 3 and 4). Virulent *A. trachoides* showed low rate of virus transmission from duranta to tomato and bell pepper. Percent transmission was relatively high between

Table 1. Occurrence of begomovirus in field sampling of *A. trachoides* infested host plants

Host plants	Samples collected	Plants (+) / No. tested
<i>Duranta</i> sp	Plant samples	25/25 (100%)
	Whitefly samples	45/75 (60%)
<i>Solanum nigrum</i>	Plant samples	0/10 (Nil)
	Whitefly samples	0/30 (Nil)
Tomato	Plant samples	2/10 (20%)
	Whitefly samples	5/30 (16%)
<i>Ipomoea</i> sp.	Plant samples	0/12 (Nil)
	Whitefly samples	0/36 (Nil)

As confirmed by PCR using begomovirus degenerate primers and ToLCNDV-specific primers.

duranta to bell pepper (26.6%) as compared to duranta to tomato (13.3%) (table 2).

3.2.2 *Virus transmission by A. trachoides from virus-infected tomato to other plants*: Presence of virus in inoculated tomato plant was confirmed by RCA. The DNA fragment from RCA was sequenced and submitted to NCBI GenBank (Accession No. MN166094). The sequence showed similarity with DLCV isolate 57SA segment of DNA-A (NC_038980.1) (figure 2 and supplementary table 3). Same virus positive tomato plant was used for all the further transmission studies.

The transmission rate was 80% in case of tomato to tomato and 100 % in case of tomato to bell pepper and tomato to potato (table 2). The primary PCR results of virus inoculated potato, tomato and bell pepper showed faint virus bands with both Deng degenerate primers and ToLCNDV specific primers. The virus was detected conclusively only when secondary PCR was performed using tenfold diluted primary PCR product as template (figure 3 and 4).

The consensus sequences derived from Deng degenerate primers amplified fragments of *A. trachoides*, duranta, bell pepper, tomato and potato inoculated with DLCV by *A. trachoides* showed 91.4 to 94 % sequence similarities with PLCV (HM140368.1) and 89.4 to 93.9 % similarity with DLCV isolate 57SA segment DNA-A (NC-038980.1) (supplementary table 4). These results confirmed the successful acquisition and transmission of virus by *A. trachoides* to tomato, bell pepper and potato.

3.3 Detection of β satellite

The virus positive plants and *A. trachoides* tested positive for the β satellite and showed ~1.3 kb DNA amplicon using universal primers (supplementary figure 2).

Table 2. Duranta leaf curl transmission by *A. trachoides*

Host plants	Plants (+) / No. Inoculated (%)
Duranta to tomato	2/ 15 (13.3%)
Duranta to bell pepper	4/15 (26.6%)
Tomato to tomato	12/15 (80%)
Tomato to bell pepper	15/15 (100%)
Tomato to potato	15/15 (100%)

Transmission confirmed by PCR using degenerate primers and ToLCNDV specific primers.

4. Discussion

Until now *A. trachoides* was not known to transmit any of the plant virus. It only caused direct damage by feeding on plants in addition to the excretion of honeydew, which promotes the growth of sooty mould (EPPO 2017). *A. trachoides* as vector of begomoviruses as observed in the present study will have huge consequences. Since, *A. trachoides* feeds on several important plants, such as bell pepper, hot pepper, potato, sweet potato, tobacco, avocado, rose, tomato, eggplant, commercially important trees like *Santalum album*, *Tabebuia argentea*, *T. impetiginosa*, *T. rosea*, coconut palm and *Vitex leucoxylon* (EPPO Global Database 2016; Sundararaj *et al.* 2018). Some of the host plants being perennial they may serve as permanent reservoir for *A. trachoides* as well as the virus. There are few reports of perennial trees as the hosts for begomoviruses (Sohrab 2018).

The percent transmission of DLCV was relatively low between duranta to bell pepper and tomato. However, the rate of transmission was higher from tomato to tomato, tomato to bell pepper and tomato to potato. These results suggest that once virus transmitted to tomato from duranta, its further rate of transmission by *A. trachoides* to similar hosts is very high.

All the virus-inoculated plants showed PCR amplification with ToLCNDV specific primers. These results are in consistence with reported literature (Anwar and Tahir 2018). All duranta samples showed very good amplification in primary PCR, however all inoculated plants showed faint bands in primary PCR with both the primers. Hence, secondary PCR was performed using first amplicon as template. This might be probably due to slow rate of virus multiplication in these host plants. The sequencing of DNA fragments amplified with Deng degenerate primers from virus inoculated potato, tomato and bell pepper showed more than 90% similarity with PLCV and DLCV isolate 57SA segment DNA-A. These results are in confirmation with earlier reports. Begomovirus of duranta reported to show 98 % sequence identity with PLCV (Marvel *et al.* 2013). DLCV considered as recombinant virus because its virion-sense and complementary-sense nucleotides shows different identities (Iram *et al.* 2004).

Previous studies have failed to detect α satellite and β satellite on begomovirus-infected duranta using universal primers (Marvel *et al.* 2013). However, in the present study, the amplicon of ~ 1.3 kb similar to β satellite was observed in the begomovirus-infected duranta, tomato and bell pepper plants as well as in *A.*

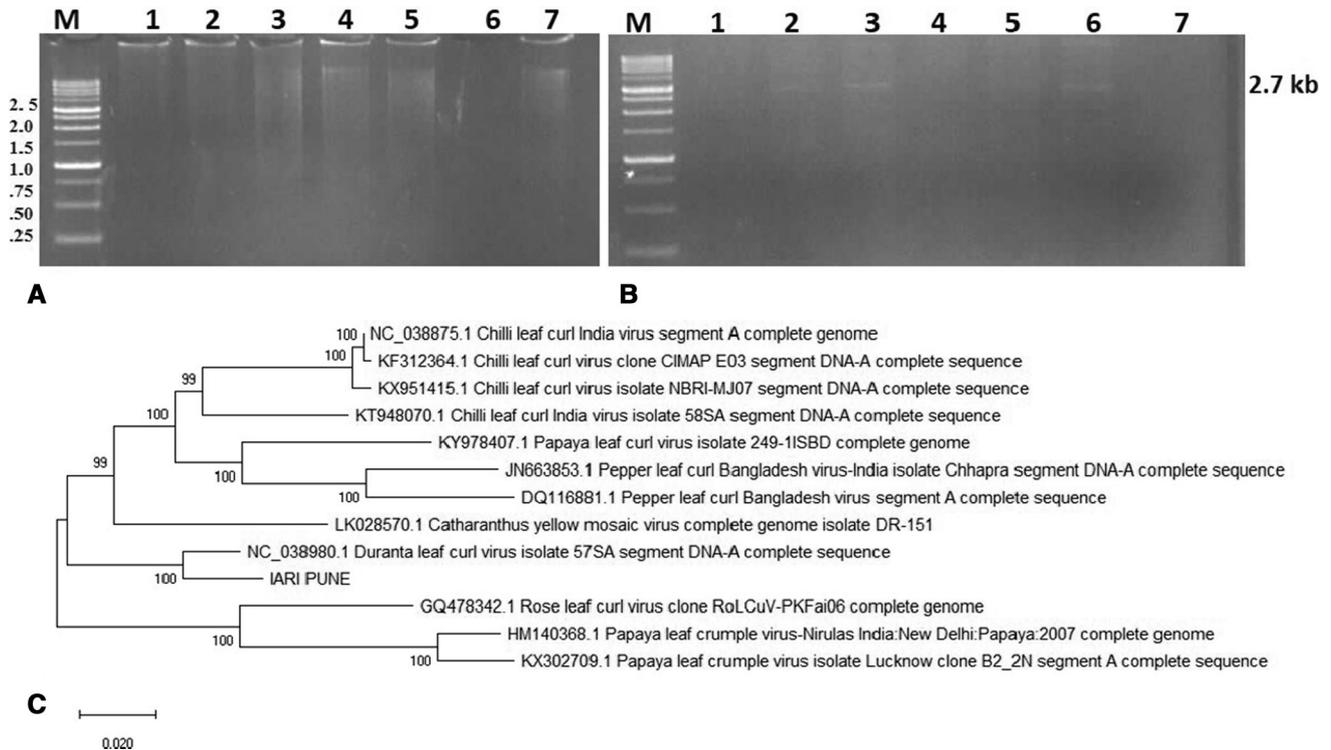


Figure 2. (A) RCA product of tomato inoculated with *Duranta leaf curl virus* by whitefly *A. trachoides*, (B) *Bam*H1-digested RCA product showing 2.7 kb fragment, (C) phylogenetic tree constructed using sequence of IARI PUNE (2.7 kb virus fragment obtained from RCA product GenBank No MN166094) showing similarity with *Duranta leaf curl virus* (NC_038980.1).

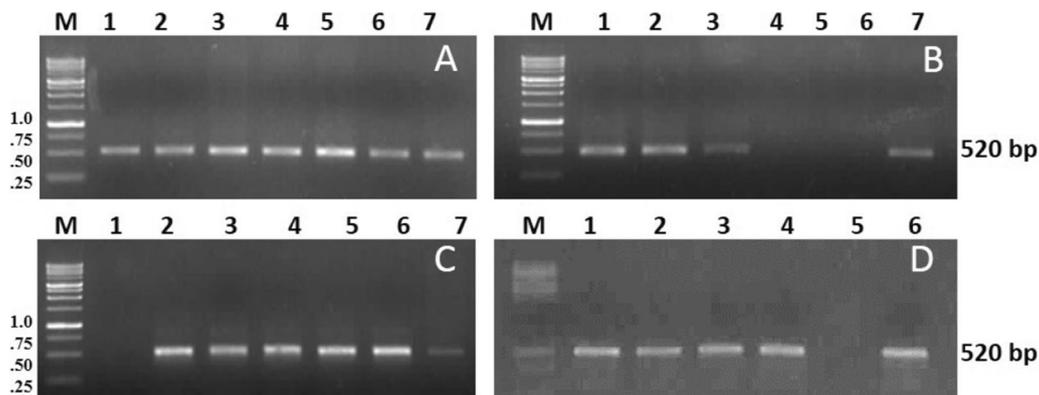


Figure 3. Deng degenerate primers amplified samples of (A) *Duranta* (lane 1–4) and whitefly (lane 5–7), (B) virus transmission by *A. trachoides* from *Duranta* to tomato (samples: lane 1, 2 and 3; control: lane 5 and 6; + control, lane 7), (C) bell pepper (samples: lane 2–6; – control, lane 1; + control, lane 7) and (D) potato (samples, lane 1–4; – and + control, lane 5 and 6).

trachoides feeding on the virus-infected plants. For some of the begomoviruses, their association with β satellite is essential for the development of disease symptoms in hosts (Briddon et al. 2001; Cui et al. 2004).

There are about 1500 known species of whiteflies, but only few are reported to transmit about 140 plant viruses.

Bemisia tabaci species complex alone transmits about 111 viruses (Jones 2003). Other known vector species are: *Parabemisia myricae* Kuwana, *Alerodies disperses*, *Trialeuro desabutlonea* and *Trialeurodes vaporariorum*. To the best of our knowledge, there are no reports available on vector status of *A. trachoides*. We observed variation in the percent transmission of DLCV by

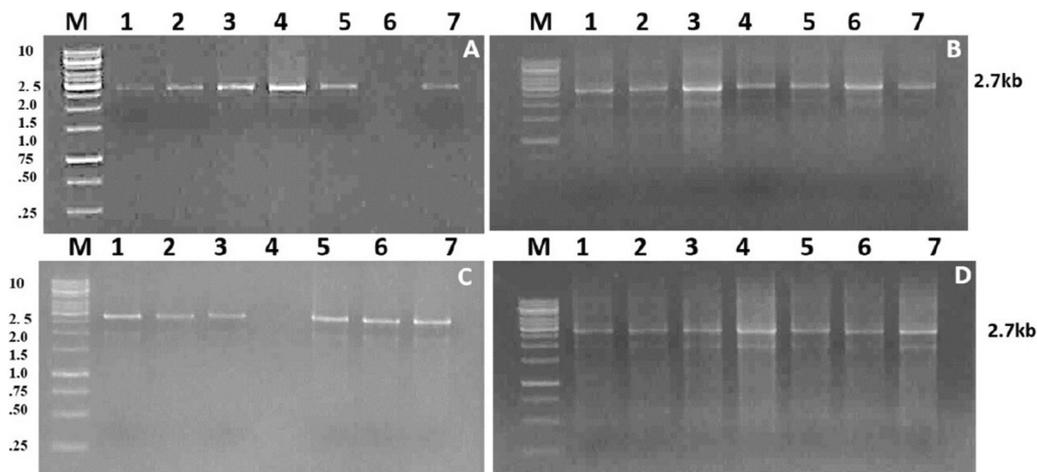


Figure 4. Amplification by ToLCNDV specific primers, (A) *Duranta* (lane 1–4) and whitefly (lane 5–7), (B) transmission of virus by *A. trachoides* from *Duranta* to tomato (samples: lane 1–6; + control, lane 7), (C) bell pepper (samples: lanes 1, 2, 3, 5 and 6; – and + control: lanes 4 and 7) and (D) potato (samples: lanes 1–6; + control: lane 7).

A. trachoides between host plants. Whitefly vectors differ in their ability to transmit different viruses. In a virus transmission study of cassava mosaic and brown streak diseases (CMD and CBSD) by three species of whiteflies, only *B. tabaci* was able to transmit CMD, whereas CBSD was transmitted by *A. disperses*, *B. tabaci* and *T. vaporariorum* (Njoroge *et al.* 2017). Rate of virus transmission by *A. disperses* was low as compared to *B. tabaci* and *T. vaporariorum*. In case of *Tomato yellow leaf curl virus*, *T. vaporariorum* show similar rates of transmission ability as that of *B. tabaci* (Lapidot 2007). Begomovirus-whitefly vector specificity depends on several factors that influence virus acquisition and successful transmission to other host. Many vector proteins are known to facilitate the transmission of begomoviruses (Varun and Saxena 2017). In absence of any prior information on *A. trachoides* as a virus vector, the present study used higher numbers of whiteflies (25/plant) and longer feeding period (72 h) for successful transmission. Further, detailed studies are required to understand *A. trachoides* relationship with begomovirus and its efficiency and impact of transmission to commercial host crops.

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