International Journal of Tropical Insect Science
https://doi.org/10.1007/s42690-021-00544-1

ORIGINAL RESEARCH ARTICLE

Incidence of the cabbage aphid, *Brevicoryne brassicae* L. in potato crops in India and its efficiency for transmission of *potato virus Y*^{o}

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Received: 22 December 2020 / Accepted: 20 April 2021

Abstract

Potato crops are infected by a large number of aphid-transmitted viruses resulting in yield loss and degeneration of seed stocks. These viruses are transmitted by a large number of colonizing and non-colonizing aphids. The non-colonizing aphid species are mainly responsible for the spread of non-persistent viruses like *potato virus Y* (PVY^{o}). The cabbage aphid, *Brevicoryne brassicae* L., an important pest of cruciferous crops, is a non-colonizing aphid visiting potato crops transiently. We evaluated the relative prevalence of cabbage aphids in potato crops at four locations namely, Jalandhar (Punjab), Shimla (Himachal Pradesh), Modipuram (Uttar Pradesh) and Kalyani (West Bengal), where most of the seed and ware potato production is carried out in India. The cabbage aphids constitute an appreciable proportion (3.57% to 19.04%) of the aphid population on potato plants at these locations. The cabbage aphids were found to successfully acquire and transmit the PVY^{o} from and to potato plants. The virus transmission efficiency came out to be 11.25%, with a relative efficiency factor (REF) of 0.13, in comparison to the peach-potato aphid, *Myzus persicae* (Sulzer). This is the first report of *B. brassicae* being a vector of PVY^{o} in India. Therefore, isolation of seed potato crops from cruciferous crops or stringent management of the aphids on the latter is necessary for production of healthy seed potatoes.

Keywords PVY^{o} · Vector · Viruliferous · Potato · Non-persistent virus · Non-colonizing aphid

Introduction

Potato is the third most important food crop globally (Singh et al. 2020). India is the second largest producer of potato in the world where it is considered important for food and nutrition security (Mhatre et al. 2020). Among the production constraints, shortage of quality potato seed is an important factor responsible for low productivity (Malik et al. 2020). Potato productivity is challenged by the incidence of a large number of aphid-transmitted viruses e.g., *potato virus Y* (PVY), *potato leaf roll virus* (PLRV), *potato virus A* (PVA) etc. in India (Raigond et al. 2020a). Among these, PVY^{o} is predominant which can cause a yield loss of 23 – 25% (Khurana and Singh 1988).

PVY^{o} is transmitted to healthy plants horizontally under field conditions by a number of colonizing and non-colonizing aphids. More than 65 aphid species or species groups are known to transmit PVY in a non-persistent manner, most of which are non-colonizing in nature (Lacomme et al. 2017). Although the peach-potato aphid, *Myzus persicae* (Sulzer) is the most efficient vector of PVY, many other species of aphids have been demonstrated to transmit the virus in potato crops in India including *Aphis gossypii* (Glover), *Macrosiphum euphorbiae* Thomas, and *Aulacorthum solani* (Kaltenbach) (Naga et al., 2020; Sridhar et al. 2020; 2021).

In India, potato is mainly cultivated in the Indo-Gangetic plains under short day conditions during winter (Shah et al. 2020). It is a common practice to cultivate many winter

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Published online: 23 April 2021

vegetables including cabbage, cauliflower, and crops like rapeseed/ mustard alongside potato crops (Shah et al. 2019). On the cruciferous plants, the incidence of the cabbage aphid, *Brevicoryne brassicae* (Linnaeus) is common (Ellis and Farrell 1995). Although it does not colonize potato plants, the cabbage aphids can visit the potato plants transiently in large numbers (Lacomme et al. 2017). The cabbage aphid has been reported to occur on potato in France (Boquel et al. 2011), in USA (Halbert et al. 2003) and in Netherlands (Verbeek et al. 2010). Lately, the cabbage aphids were detected on potato plants in appreciable numbers in the subtropical plains of India coinciding with higher incidence of potato viruses like PVY^{o}. The incidence of cabbage aphids is particularly high on the late season potato crops (February to March) (Aslam et al. 2007). Therefore, we sampled aphids from potato crops across the Indo-Gangetic plains to determine the degree of infestation of the cabbage aphid and its efficiency at transmission of PVY^{o} to understand its importance for production of healthy seed potatoes.

Materials and methods

Collection of aphid samples

Aphids were collected from potato plants at four locations namely, Shimla (Himachal Pradesh), Modipuram (Uttar Pradesh), Jalandhar (Punjab) and Kalyani (West Bengal) at multiple occasions during 2014 to 2016. In each geographic location, aphids were sampled from distant fields to enhance probability of collecting diverse species. Although, aphids were sampled from all potato growing zones of India, significant incidence of *B. brassicae* was recorded at these four locations only. Hence we have presented data pertinent to *B. brassicae* of four locations only. In each sampling bout, aphids were collected from 30 plants in each field, from three leaves selected from upper, middle and lower strata in each plant (Hafez 1961). Samples were collected on three occasions (early, mid and late) in each growing season. The aphid samples were preserved in 95% ethanol in cryo vials (5 ml), labelled for location and date of sampling and brought to laboratory.

The aphid samples were counted and sorted for *B. brassicae*. Selected specimens of apterous and alate adults of *B. brassicae* were processed and mounted on microscope slides following the standard protocols described by Foottit and Maw (2000). Identification based on morphological characteristics was undertaken using standard taxonomic keys (Blackman and Eastop 2000). Besides, specimens were sent to ICAR-National Bureau of Agricultural Insect Resources, Bengaluru, India; nodal institute for aphid identification.

Species identity was further confirmed by generating mitochondrial partial *COI* gene sequences. Total genomic DNA was isolated from individual aphid samples using DNA extraction kit (Qiagen DNeasy Blood & Tissue Kit) and was quantified using Nano drop (Thermoscientific, Leon-Rot, Germany). PCR was performed in a thermal cycler (Applied Biosystems 9700) as per the protocol of Sridhar et al. (2017). The primers used were Sense, LCO-1490; 5′-GGTCAACAAATCATAAAGATATTGG-3′ and Antisense, HCO-2198; 5′-TAAACTTCAGGGTGACCA AAAAATCA-3′ (Hebert et al. 2003). The amplified products were checked on 1.0% agarose gel which was stained with ethidium bromide (10 µg/ml) and visualized in a gel documentation system. The desired DNA fragment was sequenced by employing 3500 Genetic Analyser, Applied Biosystems (Hitachi).

Transmission studies

A single gravid female of *B. brassicae* from Shimla clone was reared on *Brassica oleracea* var. *capitata* (L.) cultivar having four fully expanded leaves in plastic pots (13 cm diameter) with a mixture of peat moss, vermiculite and organic fertilizer under controlled conditions in a glasshouse (Temperature 20 ± 2 °C; Humidity 75 ± 5%). These pots were placed in insect proof wooden cages having 60 mesh size in three sides with a glass on top and front door (60 × 60 × 90 cm) and watered regularly (Jahan et al. 2013). The insect culture was multiplied by shifting first instar nymphs on to fresh cabbage seedlings at regular intervals up to two generations. Then, the freshly formed wingless adults were used in the transmission experiments subsequently.

Pure culture of PVY^{o} was obtained from virus culture facility at ICAR- Central Potato Research Institute (CPRI), Shimla (H.P.), India. The inoculum of PVY^{o} was maintained on potato (*Solanum tuberosum* L.) and also on propagative host *i.e.*, tobacco (*Nicotiana tabacum* var. Samsun) in the glasshouse of "Virus Culture Facility" ICAR-CPRI, Shimla (H.P.), India at a temperature of 22–25 °C with natural daylight. The inoculum is multiplied/maintained/sub-cultured by mechanical inoculation. This inoculum was used as research material for the acquisition of PVY^{o} by *B. brassicae*.

Tissue culture raised healthy seedlings of potato cv. *Kufri Pukhraj* obtained from Division of Seed Technology, ICAR-CPRI, Shimla were raised in pots with sterilized soil in a glasshouse under controlled conditions. Then the pots were placed in insect proof cages for further transmission studies. These seedlings were tested for PVY^{o} prior to transmission study to confirm freedom from virus infection. Seedlings free from PVY^{o} were utilized as test plants in virus transmission studies. Five sets of 16 plants each, 4 weeks old, were used in the transmission study separately with *B. brassicae* and *M. persicae*.

Aviruliferous wingless adults of *B. brassicae* were collected from the stock culture, starved for 3 h for better

acquisition and then released on plant infected with PVY^{o} for a duration of 24 h for virus acquisition i.e., acquisition access period (AAP) (Raigond et al. 2020b).

Virus acquisition by aphid vector becomes crucial in transmission efficiency studies. To confirm virus acquisition, we selected 3–5 aphids randomly after AAP and RNA was isolated and reverted to cDNA. The coat protein gene of PVY^{o} was amplified following standard protocols which confirmed its acquisition by *B. brassicae* (Venkateswarlu et al. 2016; Sridhar et al. 2020).

Five viruliferous individuals of *B. brassicae* were released on each healthy potato plant for 24 h inoculation access period (IAP). Afterwards, the adults were removed from the potato plants and the plants were sprayed with imidacloprid 17.8 SL @ 0.03% to kill any nymphs laid. All the transmission experiments were carried out under controlled conditions i.e. temperature 23 ± 1 °C and relative humidity 70 ± 5%.

The potato plants were examined for expression of visual symptoms (mild mosaic, veinal chlorosis, crinkle and leaf curling) at weekly interval for four weeks. The plants with symptoms of virus infection were counted in each observation.

To confirm the presence of PVY^{o}, leaf samples were collected from all the plants and tested using RT-PCR at weekly intervals following standard protocols (Raigond et al. 2014; Sridhar et al. 2020). The coat protein gene of PVY^{o} was amplified using primers, sense, PVY-FCP; 5′-ACGTGGTATGAGGCAGTGCGGA-3′ and antisense, PVY-RCP; 5′-ATGTGCGCTTCCCTAGCCCTCA-3′. PCR conditions were followed as per protocol of Venkateswarlu et al. (2016). The reaction mixture (Make: Invitrogen Bioservices India Pvt Ltd, Bengaluru) consisted of 20 µl containing 2.5 µl of 10 × Taq buffer A, 1.5 µl of 2 mM dNTP mix, 1.0 µl of 10 pM forward and reverse primers each, 2 µl of cDNA template, 1.0 µl of 1.0 U/µl of Taq DNA polymerase and 11 µl sterile nano pure water. PCR reaction was carried as follows; initial denaturation at 94 °C for 2 min, 94 °C for 30 s, annealing temperature at 62 °C for 45 s, followed by extension at 72 °C for 35 cycles of 1 min along with final extension step at 72 °C for 5 min. The amplicons were resolved in 1.0% agarose gel, stained with ethidium bromide (10 µg/ml) and visualized in gel documentation system.

Additionally, PVY^{o} virions were detected in test plants under immunosorbent transmission electron microscop (TEM) at ICAR-CPRI, Shimla using standard protocols (Garg and Khurana 2003).

A parallel experiment was set up for *M. persicae* to calculate relative efficiency factors (REF) of *B. brassicae* according to Verbeek et al. (2010): where REF is given by: REF (clone) = % Infected plants (clone)/% infected plants (*M. persicae*).

Results

To assess the incidence of cabbage aphids in potato crops, aphid samples were collected from potato crops from four different locations, namely Shimla, Jalandhar, Modipuram and Kalyani of India. The potato growing season in these locations coincided with cabbage crop as these crops are raised during winter months in Indo-Gangetic plains of India. The relative proportion of the cabbage aphid among total aphid populations on potato plants was 11.90%, 3.57%, 5.88% and 19.04% at the four locations, respectively (Fig. 1).

The cabbage aphids were identified with diagnostic characteristics including the presence of dark head, thorax and abdominal sclerites, barrel shaped siphunculi and triangular cauda in apterae, while as the alatae had 50 – 70 secondary rhinaria on third antennal segment with dark abdominal cross bands (Blackman and Eastop 2000). The species identity of *B. brassicae* was further confirmed by nodal institute, ICAR-National Bureau of Agricultural Insect Resources, Bengaluru, India. The morphological identification was authenticated by sequencing 657 bp amplicon of mitochondrial CO1 gene. The nucleotide sequences of the present study have been deposited in the National Center for Biotechnology Information GenBank database (KY586086 to KY586091). These sequences showed 98–100% similarity with reported sequences of *B. brassicae* in the database which confirmed the species identity. The consensus on the identity of *B. brassicae* were arrived as these sequences showed very high similarity with populations of other parts of India (Bengaluru), China, USA, Canada, Kenya and Australia. A Neighbour Joining tree was drawn to understand

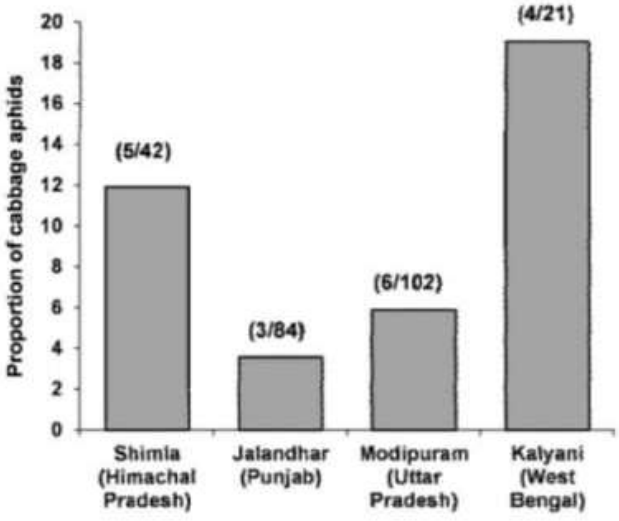

Fig. 1 Prevalence of *Brevicoryne. brassicae* on potato at four different locations in India. Figures in parentheses indicate the number of cabbage aphids out of the total number of aphids sampled

the identity of *B. brassicae* and its relationship with similar populations from different countries using the neighbor joining method (Fig. 2). The cabbage aphid COI sequences were found to form two distinct clusters. The intraspecific COI sequence divergences ranged from 0.00 to 0.038% with a mean of 0.02%.

Out of the twenty sets of randomly selected aphids from each acquisition trial, more than 95% of the aphid samples tested positive for PVY^{o}, indicating successful acquisition of the virus. The typical symptoms of PVY^{o} were first noticed two weeks after inoculation on the leaves of test plants, the severity of which increased till the 4th week. The results revealed that only 2 test plants showed symptoms in 2nd week, while as, by the 3rd and 4th week, 5 and 9 plants out of 80 expressed mild symptoms of PVY^{o} infection, respectively.

The virus was not detected in RT-PCR in test plants during first week after IAP with viruliferous cabbage aphids. However, PVY^{o} was detected in test plants two weeks post inoculation and the number of test plants testing positive for the virus increased till the 4th week. After 4 weeks of inoculation with viruliferous cabbage aphids, 11.25 ± 1.25% (mean ± SE) of test plants tested positive for PVY^{o}. In parallel experimental setup, 85 ± 3.75% of the test plants inoculated with viruliferous peach-potato aphids tested positive for PVY^{o} (Fig. 3).

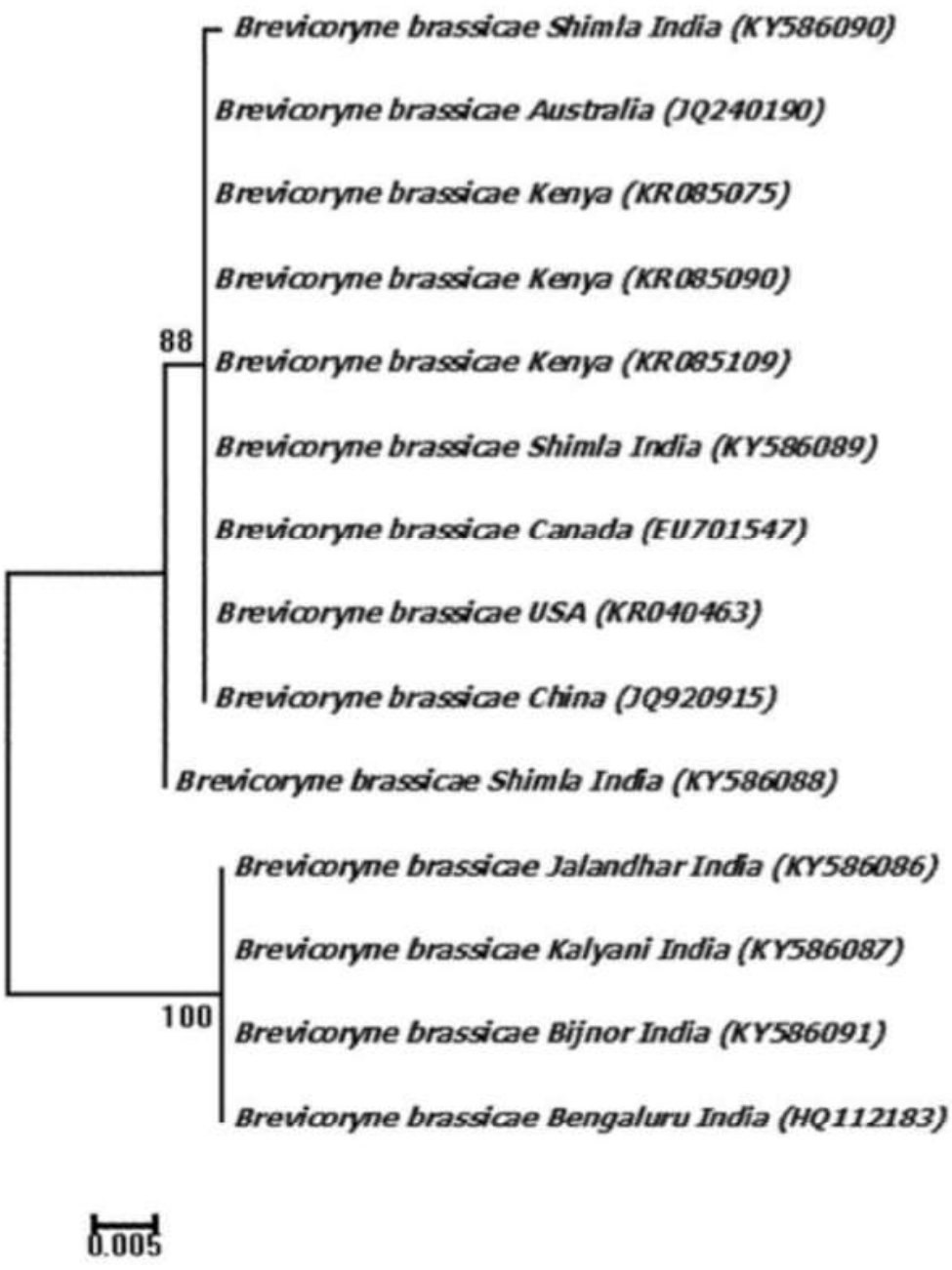

Fig. 2 Neighbor joining tree showing genetic relationships of *Brevicoryne brassicae* collected from potato based on partial COI sequences. Numbers shown next to the branches are bootstrap values (1,000 replicates) obtained with Kimura 2-paramter (K2P) distance

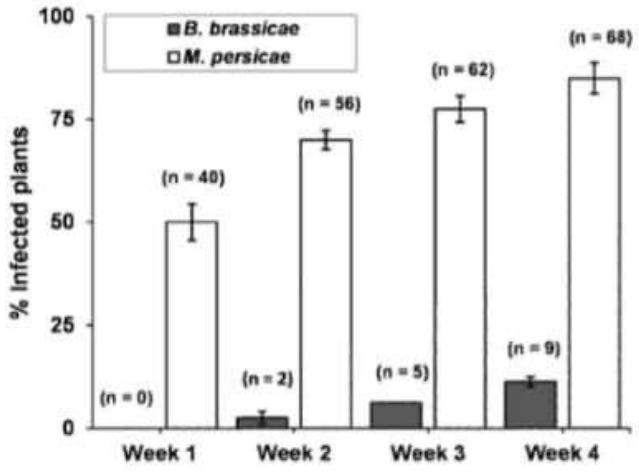

Fig. 3 Weekly infection rate of potato plants inoculated with PVY^{0}-carrying *Brevicoryne brassicae* and *Myzus persicae* (*n* is the total number of plants tested positive for PVY^{0} out of a total of 80 plants)

The immunosorbent transmission electron microscopy based detection of PVY^{0} in test plants was done to strengthen the identity of virus. The flexuous virus particles were clearly observed under TEM that confirmed virus identity (Fig. 4).

The REF of *B. brassicae* with respect to PVY^{0} was determined by comparing its virus transmission efficiency with that of *M. persicae*. The REF of *B. brassicae* came out as 0.13 in the present study.

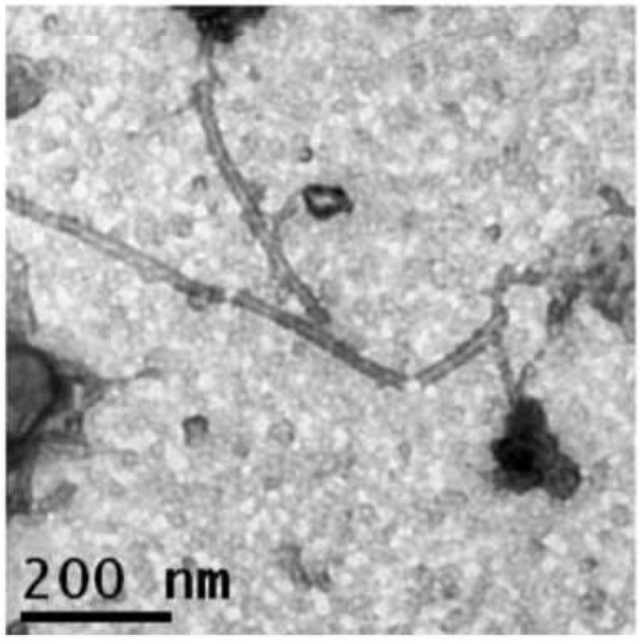

Fig. 4 The potyvirus-like virions from test plants trapped and decorated with homologous antiserum clumped with PVY^{0} antiserum (bar = 200 nm)

Discussion

Non-colonizing species of aphids are important for the field spread of non-persistent potato viruses like PVY^{0}. We found that the cabbage aphids constitute an appreciable proportion (3.57% to 19.04%) of the aphid population in potato crops in the selected locations. The cabbage aphids are abundant on the cole crops like cabbage, cauliflower, and rapeseed/mustard (Yadav and Rathee 2020) which are mostly grown alongside the potato crops in India and hence become important sources of the aphid. Due to their non-colonizing nature on potato (Boquel et al. 2011), the cabbage aphids visit the potato crops transiently and can potentially lead to spread of viruses like PVY^{0}. Cabbage aphids are reported to infest potato crops in France (Boquel et al. 2011), USA (Halbert et al. 2003) and Netherlands (Verbeek et al. 2010). In general, PVY transmission by aphids in non-persistent manner needs just few second to probe and acquire the virus and immediately inoculate healthy plants and it doesn't need longer AAP and IAP. Also, the inoculum load gradually decrease and is lost when the same insects probe further plants (Fereres and Moreno 2009).

The cabbage aphids successfully transmitted PVY^{0} from infected to healthy potato plants. The virus transmission efficiency came out to be 11.25%, with a relative efficiency factor (REF) of 0.13, in comparison to the peach-potato aphid. Present study reports slightly higher PVY^{0} transmission rate and REF of *B. brassicae* in comparison to earlier studies. Sigvald (1992) attributed a REF of 0.01 to *B. brassicae* for transmission of PVY^{0}. Boquel et al. (2011) observed that *B. brassicae* was a poor vector of PVY (REF 0.04) as compared to *M. persicae*. In many other reports, the cabbage aphids collected from potato plants were not found to transmit PVY^{0}, PVY^{N} and PVY^{NTN} strains under controlled conditions (Sigvald 1984; Halbert et al. 2003; Basky and Almasi 2005; Verbeek et al. 2010; Fox et al. 2017).

In general, the cabbage aphids are known as poor vectors of potato viruses. The probing behavior of the cabbage aphid differs from most aphid vectors as it rarely probes leaf tissue; shows little adaptability to plant-to-plant transference techniques and is apparently immune to the pre-acquisition starvation effect (Van Hoof 1954). However, a higher number of aphids visiting potato crops can compensate the weak transmission efficiency, as in the case with most of the non-persistent aphids (Katis et al. 2006; Boquel et al. 2012). Therefore, it would be advisable not to grow cabbage aphid supporting crops like cruciferous vegetables etc. in close vicinity of seed potato crops or else, the aphid pest must be stringently managed on such crops.

Further, the NJ tree analysis of COI sequences showed similarity of the cabbage aphids with the populations in

the USA (KRO40403), Australia (JQ240190), Canada (EV701547) and China (JQ920915). The cabbage aphids collected from four locations were found to form two distinct clusters, indicating possibility of cryptic species. Rebijith et al. (2013) reported the existence of two sibling species of cabbage aphids in Karnataka (India) on *Raphanus sativus*. Similarly, two biotypes, NZ-1 and 2, of cabbage aphids were previously reported by Lammerink (1968) based on field experiments. Therefore, it is most probable that cabbage aphid is a cryptic species in India. It would be of interest to see if the sibling species of *B. brassicae* differ with respect to morphometric characteristics, host plant adaptation and virus transmission efficiency.

To conclude, the present study confirmed the prevalence of *B. brassicae* on potato and its ability to transmit PVY^{o} under Indian conditions. The cabbage aphids were found to transmit PVY^{o} with an efficacy of 11.25%, and REF of 0.13. Besides, the *B. brassicae* was found to group in to two distinct clusters based on COI nucleotide sequence which points at the possibility of the aphid being a cryptic species in India as well.

Acknowledgement The authors are grateful to Dr. Sunil Joshi, ICAR-NBAIR, Bengaluru for his help in identification of the aphids.

Authors' contributions JS, MN and SKC conceived the problem. JS, AB and VV planned the research. JS, BR, VV, AB and MAS collected and curated the aphid samples. JS, NK did the molecular analysis. BR did Transmission electron microscopic studies. NK, JS and MAS wrote the manuscript. MN, SKC, BR edited and improved manuscript critically All authors commented on the draft and approved for publication.

Funding This work was funded by the Indian Council of Agricultural Research, New Delhi, India, through an institute research project (HORTCPRICIL201500600134).

Data availability The data are available from the first author (JS) upon reasonable request.

Code availability The data are available from the first author (JS) upon reasonable request.

Declarations

Consent for publication All authors approved the MS for publication.

Conflicts of interest The authors declare that they have no conflict of interest.

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