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REVIEW

Genetics of *Thrips palmi* (Thysanoptera: Thripidae)

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Abstract
Melon thrips (*Thrips palmi*) is the principal insect pest of vegetable and ornamental plants worldwide. In addition to inflicting feeding injuries on host plants, they act as vectors of economically damaging tospoviruses. Application of insecticides and host plant resistance has proven largely ineffective in the management of *T. palmi*. However, increasingly, genetic knowledge is being successfully utilized to manage insect pests. A number of recent studies have enriched the genetic database of *T. palmi*. In this review, we report on genetics of *T. palmi* for species identification and to study its populations structure. For example, a DNA polymorphism analysis of global *T. palmi* populations has revealed the existence of 29 haplotypes. The *T. palmi* population can be divided into three lineages based on phylogenetic analysis. A high maximum intraspecific distance is indicative of cryptic species within *T. palmi* populations. Regarding climate adaptability, the upregulation of trehalose biosynthesis genes, and genes encoding several heat-shock proteins is expected to enable *T. palmi* thermal adaptation to both cold and hot conditions. Genetics of *T. palmi* has shown that resistance to conventional insecticides like cypermethrin appears to be linked to mutations in the sodium channel. On the other hand, resistance to imidacloprid appears to be a result of cytochrome P450-mediated detoxification. *T. palmi* genes potentially involved in tospovirus transmission are also reviewed and new molecular tools for genetic study presented. Molecular modeling and docking analyses of groundnut bud necrosis virus glycoprotein demonstrated protein–protein interactions with *T. palmi* vacuolar ATP synthase E subunit, cathepsin, clathrin, adaptor protein 2, and enolase. Overall, a better knowledge of *T. palmi* genes will assist elucidation of thrips identification, means of adaptation in diverse ecological niches, mechanisms of insecticide resistance, and transmission of plant viruses. This data will be an invaluable tool for integrated thrips management.

Keywords Melon thrips · Haplotype · Identification · Adaptation · Insecticide resistance · Tospovirus transmission

Key message

- DNA polymorphism analysis indicates 29 haplotypes of *T. palmi*
- Possible involvement of glycerol and mannitol as cryoprotectants in cold-exposed *T. palmi*
- Resistance in *T. palmi* against cypermethrin due to mutations in the sodium channel
- Imidacloprid resistance in *T. palmi* as a result of CYP450-mediated detoxification
- C-type lectin appears to be the first known cellular receptor in *T. palmi* with which groundnut bud necrosis virus G_N protein interacts followed by clathrin-mediated endocytosis

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Introduction

Thrips palmi (Thysanoptera: Thripidae), commonly known as melon thrips, is a major pest of vegetable and ornamental plants worldwide. It causes economically significant losses particularly in Cucurbitaceae, Solanaceae, Fabaceae,

and Asteraceae families (http://entomology.ifas.ufl.edu). The extremely small (0.8–1.0 mm length) sized nymphs and adults feed on plants by sucking the cell contents from leaves, stems, flowers, and the surface of fruit. Infested plant parts develop silvery scars and chlorosis. Deformities, abortion of fruit, and death of plants are also observed in some cases (Childers 1997; Ghosh et al. 2009). Apart from the direct injuries caused by feeding, thrips inflict indirect damage by transmitting destructive plant viruses. Among them, groundnut bud necrosis virus (GBNV) is considered to be the most destructive tospovirus transmitted by *T. palmi* in vegetable and ornamental crops. It causes economic losses of US$ 89 million annually in Asia with 70–90% yield loss in groundnut and 30% in potato in India (Reddy et al. 1995; Singh and Srivatava 1995; Singh et al. 1997; Daimei et al. 2017). On the other hand, watermelon bud necrosis virus (WBNV), also transmitted by *T. palmi*, causes crop losses of US$ 50 million annually (Rebijith et al. 2016).

T. palmi was first described in Indonesia in 1925 and was later recorded in India, Sudan, and Taiwan (Cannon et al. 2007). It is now widely distributed across southeast Asia, Oceania, Pacific islands, Australia, the Americas, the Caribbean, and Africa (Table 1). Its broad thermal adaptability has helped *T. palmi* to establish in diverse climatic conditions. Outbreaks of *T. palmi* in aubergine, capsicum, cucumber, melon, potato, snap bean, sweet pepper, and watermelon have raised serious concerns regarding conventional management practices (Cannon et al. 2007). Application of insecticides, host plant resistance, augmentation of natural enemies as the core components for thrips management is largely ineffective. Exploitation of the genetic information of the insects in pest management has shown promising results (Grimmelikhuijzen et al. 2007; Mouden et al. 2017). For example, genetic information on *Frankliniella occidentalis* (Western flower thrips) has led to the development of an RNA interference tool for its management (Badillo-Vargas et al. 2015; Whitten et al. 2016). Comparative transcriptome analyses of tomato spotted wilt virus (TSWV)-infected and non-infected *F. occidentalis* facilitated identifying thrips effectors suppressing or inducing plant defence responses (Stafford-Banks et al. 2014). In the last couple of years, quite a few studies have contributed to the growing gene database of *T. palmi*. These data are of paramount importance to elucidate *T. palmi* systematics, evolution, biology, and

Table 1 Geographical distribution of *T. palmi*

Country/region	Year[a]	Country/region	Year[a]	Country/region	Year[a]
Asia		*North America*		*Central America and the Caribbean*	
Bangladesh	1974	Mexico	2004	Antigua and Barbuda	1989
Brunei Darussalam	1978	USA	1982	Bahamas	1995
China	1997	*South America*		Barbados	1994
Hong Kong	1972	Brazil	1995	British Virgin Islands	1996
India	1955	Colombia	1997	Costa Rica	2008
Indonesia	1925	French Guiana	1995	Cuba	1997
Iraq	2012	Guyana	1991	Dominica	1994
Japan	1978	Suriname	2001	Dominican Republic	1989
Korea	1993	Venezuela	1990	Grenada	1994
Lao	2014	*Oceania*		Guadeloupe	1985
Malaysia	1992	America Samoa	1998	Haiti	1992
Myanmar	1985	Australia	1989	Jamaica	1996
Pakistan	1951	French Polynesia	1989	Martinique	1985
Sri Lanka	1991	Guam	1991	Netherlands Antilles	1994
Taiwan	1979	Micronesia	1997	Puerto Rico	1987
Thailand	1973	New Caledonia	1999	Saint Kitts and Nevis	1989
Vietnam	2008	Palau	1995/1998	Saint Lucia	1994
Africa		Papua New Guinea	1997	Saint Vincent and Grenadines	1995
Côte d'Ivoire	2000	Samoa	1995/1998	Trinidad and Tobago	1989
Mauritius	1986	Wallis and Futuna Islands	1978		
Nigeria	1974				
Réunion	1986				
Sudan	1980				

EPPO global database (https://gd.eppo.int)

[a]Introduction or first report

diverse physiological mechanisms. The aim of this review is to summarize the genetic information currently available for *T. palmi*. The information is categorized by its applications in identification of *T. palmi* as well as its cryptic species and haplotypes, adaptation to diverse ecological niches, mechanisms of insecticide resistance and transmission of plant viruses.

Genetics of *T. palmi* to aid thrips species identification

Methods used for *T. palmi* identification

Accurate identification of thrips species is crucial in formulating appropriate pest management strategies and in distinguishing insects of quarantine concern from endemic species. The morphometric key-based thrips identification is largely based on characteristics of adults and is time-consuming (Sartiami and Mound 2013). Molecular diagnostic tools, derived from nucleotide sequence information, have simplified the identification of many insects including thrips, irrespective of their developmental stages, and made diagnosis more accurate and rapid. This approach of species discrimination based on their genomic DNA is highly reliable and also can be employed to resolve species ambiguities which is often not possible with morphology-based classical taxonomy. Nucleic acid and protein-based techniques such as polymerase chain reaction (PCR) based on species-specific primers, random amplified polymorphic DNA (RAPD), sequence-characterized amplified regions (SCAR) markers, quantitative PCR, loop mediated isothermal amplification (LAMP), and monoclonal antibodies have been used for identification of *T. palmi*.

In the case of thrips, nucleotide sequences of several genomic regions have been utilized for species discrimination and phylogenetic analyses (Brunner et al. 2004; Asokan et al. 2007; Inoue and Sakurai 2007; Hoddle et al. 2009; Buckman et al. 2013). Among thrips genes, the mitochondrial cytochrome c oxidase I gene (COI) is the most extensively used due to its wide acceptance as a universal barcode (Hebert et al. 2003a). Utilization of COI for large-scale DNA barcoding was first proposed in 2003 (Hebert et al. 2003a, b). Availability of robust universal primers for COI and a significant range of the phylogenetic signal in the mitochondrial COI-5′ region contributed to making COI a natural choice for barcoding (Folmer et al. 1994). The first molecular study of thrips based on the partial sequence of COI was reported in 1998 (Crespi et al. 1998), whereas the characterization of COI of *T. palmi* was published for the first time in 2002 (Brunner et al. 2002). Since then, about 250 nucleotide sequences of *T. palmi* COI have been submitted to the National Center for Biotechnology Information (NCBI) database to date. Such a high number of COI sequences have made the identification of *T. palmi* easy, irrespective of its wide geographical distribution and broad host range (Ghosh et al. 2017). Moreover, development of species-specific primers for the COI region allowed direct and rapid identification of *T. palmi* by conventional PCR (Rebijith et al. 2012). *T. palmi*-specific TaqMan probe and primers for the COI region have also been used for rapid and sensitive species identification of all developmental stages. Quantitative PCR (qPCR) was found to be extremely sensitive as it gave clear detection even with the DNA equivalent to 1/1000th of a *T. palmi* individual (Kox et al. 2005). QPCR could distinguish *T. palmi* from 23 other thrips species and also identified individuals originating from different geographical locations. Furthermore, the superior sensitivity of qPCR was able to detect and identify the eggs of *T. palmi* present in imported material (Kox et al. 2005).

The non-coding sequence of the nuclear ribosomal region named the internal transcribed spacer 1 (ITS1), ITS2, and histone H3 has also been used for identification of thrips. ITS region refers to the chromosomal spacer DNA situated between the small-subunit ribosomal RNA (rRNA) and large-subunit rRNA genes. This hypervariable region exhibits additional advantages for identification of thrips at species level because of a larger interspecific sequence distance than the COI (Glover et al. 2010). To date, about 70 sequences of *T. palmi* rRNA have been deposited in the NCBI database. The species-specific primers for *T. palmi* based on ITS1 region efficiently distinguish it from other thrips species (Yeh et al. 2014). Similarly, ITS2 has also been used for detection of *T. palmi* in a multiplex PCR assay (Nakahara and Minoura 2015). A fast, specific, and sensitive protocol has been developed for simultaneous discrimination between *T. palmi* and *F. occidentalis* by qPCR based on 5.8S-ITS2 ribosomal DNA (rDNA) region. Since 5.8S-ITS2 rDNA sequence is highly conserved for different geographical isolates of these two thrips species, this assay has been utilized to classify the geographical haplotypes (Przybylska et al. 2017). LAMP assay targeting rDNA region of *T. palmi* could efficiently distinguish it from 15 other thrips species. The high sensitivity of this LAMP assay allowed detection of samples equivalent to 2×10^{-8} larvae (Przybylska et al. 2015). On the other hand, the efficiency of histone H3 gene amplification was inadequate for haplotype determination in *T. palmi*. Although histone H3 was previously targeted for species-level discrimination in scale insects and *Drosophila* (Matsuo 2000; Unruh and Gullan 2008), it showed an overlap of interspecific and intraspecific distances in case of *T. palmi* leading to no barcode gap, and all the individuals of *T. palmi* clustered together in a NJ tree (Glover et al. 2010). This suggests that H3 region may be used for distinguishing discrete genera rather than species-level studies across a genus.

Other technique such as RAPD was also used to distinguish thrips species (Bayar et al. 2002). SCAR markers developed from RAPD have been used for developing species-specific PCR assays (Paran and Michelmore 1993). This approach was used to identify a SCAR marker from *T. palmi* that amplified a unique region of 637 bp. This gene region in *T. palmi* was further used to develop a species-specific qPCR assay (Walsh et al. 2005). A study to determine the phylogenomic relationships between major insect lineages included a non-annotated transcriptome of *T. palmi* but only used selected protein-coding genes for phylogenetic analysis (Misof et al. 2014). In another study, two unique proteins of 270–280 kDa and 290–300 kDa in size were observed in *T. palmi* extracts by gradient SDS–polyacrylamide gel electrophoresis. Based on the presence of these unique proteins, monoclonal antibodies were developed for the detection of *T. palmi* (Banks et al. 1998).

Investigation of genetic structure of *T. palmi* populations

COI sequences have also been used for detection of various thrips haplotypes and cryptic species (Glover et al. 2010; Rebijith et al. 2014; Iftikhar et al. 2016; Tyagi et al. 2017). The mitochondrial genes of thrips are known to evolve at a relatively fast rate (Shao and Barker 2003). The use of COI-5′ region in assays to detect cryptic species of insects including thrips has been well demonstrated (Hebert et al. 2004; Glover et al. 2010; Rebijith et al. 2014; Iftikhar et al. 2016; Tyagi et al. 2017; Lee et al. 2017). Based on COI sequences, putative cryptic species in *T. palmi* were first proposed in 2010. However, based on other DNA loci studied in this case, all the thrips formed a single clade with high interspecific variations. This indicated the presence of a distinct mitotype or COI haplotype in *T. palmi* (Glover et al. 2010). In another study, the maximum intraspecific distance within a *T. palmi* population was 7.6%, whereas the minimum interspecific distance was 12.6% based on COI-5′ sequence. This *T. palmi* population was divided into two lineages considering COI-5′ region as well as COI-3′ region in phylogenetic analyses. COI-5′ sequence analysis further revealed 23 haplotypes of *T. palmi* globally (Iftikhar et al. 2016). Recently, eight haplotypes (H9-H10, H126-H131) of *T. palmi* were reported in India based on COI-5′ sequence divergence (Tyagi et al. 2017). These haplotypes formed three distinct clades in phylogenetic analyses representing three molecular operational taxonomic units. A high mean intraspecific distance (0.0829) has been observed in *T. palmi*, suggesting the presence of cryptic species (Tyagi et al. 2017). A neighbor joining (NJ) analysis of all available COI sequences of *T. palmi* showed that the global *T. palmi* population can be separated into three major clades (Fig. 1). Three isolates, one each from China, Pakistan, and India branched separately. A high mean intraspecific distance (0.0621) was observed within the *T. palmi* population. Further, a haplotype data file has been generated for all these COI sequences of *T. palmi* using DnaSP6 (Rozas et al. 2017). DNA polymorphism analysis revealed 29 haplotypes (standard deviation of diversity 0.015) of *T. palmi* globally. To understand the relationship between the haplotypes, a minimum spanning network has been constructed using PopART 1.7 (Leigh and Bryant 2015). The relationship of different *T. palmi* haplotypes based on COI sequences is visualized in Fig. 2. Sequences with unverified species assignment and potential contaminants were not considered here. In the present analysis, the most common haplotype ($n = 121$) is shared among populations from India, Pakistan, Japan, Thailand, Dominican Republic, China, USA, and Taiwan. The next common haplotype ($n = 71$) occurred in India, Pakistan, and Bangladesh. There were two more low-frequency haplotypes recorded from India. All the Indonesian isolates formed a separate haplotype. Other than these, few more (~ 18) singleton clusters have been observed (Fig. 2).

Besides COI, COII sequences were analyzed for substantiating *T. palmi* haplotypes. A distinct overlap between intra- and interspecific distances was observed. *T. palmi* individuals were divergent in the COII NJ analysis which indicated the possibility of cryptic species (Glover et al. 2010). Several studies also used COIII sequences to discriminate insect species (Vogler and Welsh 1997; Kain et al. 1999). So far, 29 sequences of COIII from *T. palmi* are available at NCBI. Based on COIII analysis, *T. palmi* individuals did not cluster separately and showed very high interspecific distances making this DNA marker a suitable candidate for discrimination of thrips at the species level (Glover et al. 2010).

In conclusion, identification of *T. palmi* based on morphological characters is restricted to specific developmental stages and is time-consuming. Availability of a large number of nucleotide sequences of mtCoI, ITS, and other genome regions of *T. palmi* makes identification much easier, accurate, and rapid. This will benefit discriminating *T. palmi* from other species and has an enormous prospect in pest quarantine and management. Furthermore, the detection of cryptic species of *T. palmi* became possible based on the COI 5′ sequence divergence. However, the biological traits of these cryptic species need to be correlated. Linking the cryptic species with their functional traits especially insecticide resistance and virus transmission will be highly important.

Climate adaptability of *T. palmi*

Abiotic factors play an important role in the lifecycle and adaptability of insects. Limited information is available on the genetic basis of *T. palmi* adaptability to diverse

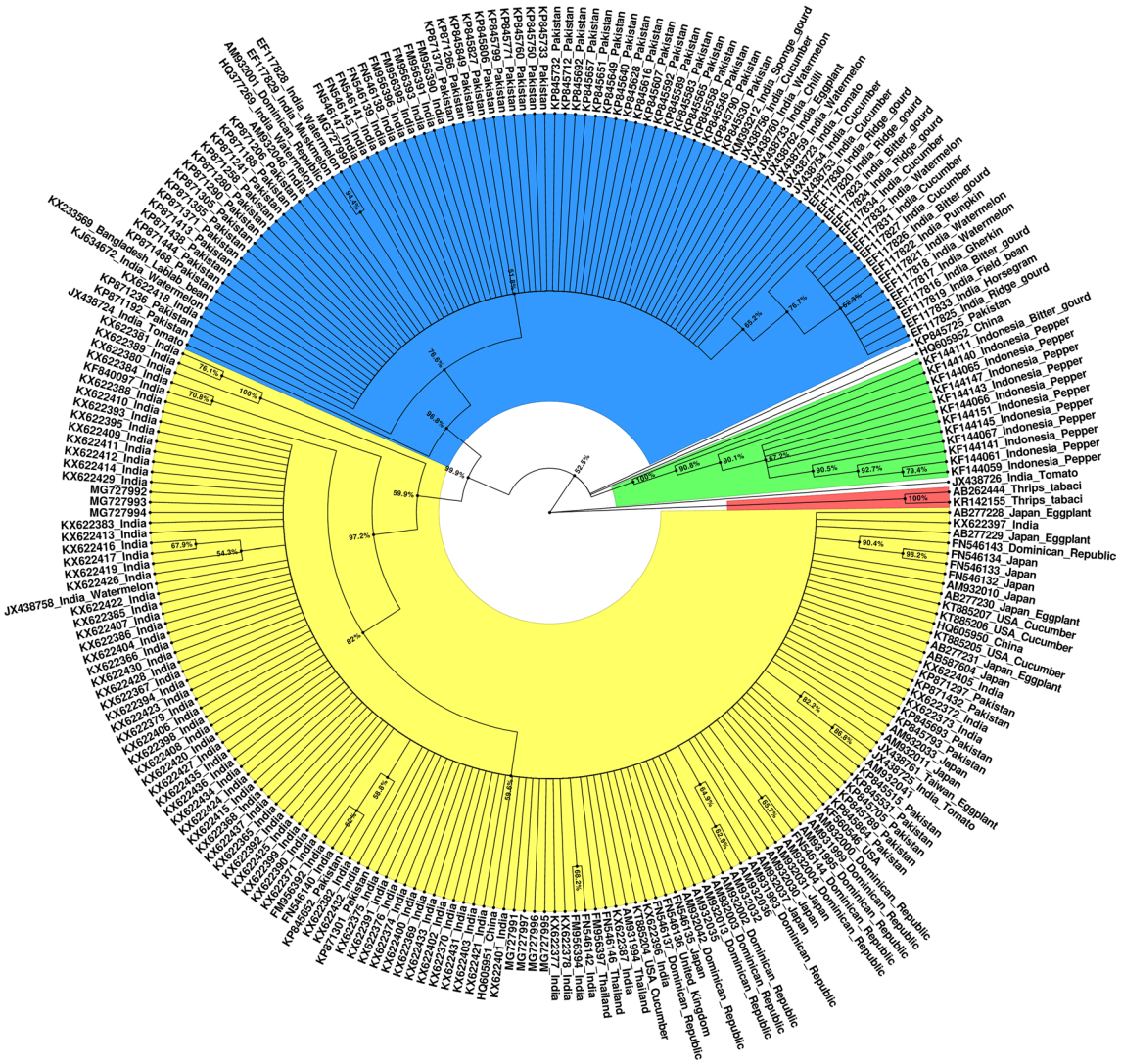

Fig. 1 Neighbor-Joining tree of cytochrome c oxidase I sequences of *Thrips palmi*. Two hundred and fifty sequences were available in NCBI database as of April 30, 2018. Sequences were aligned by MUSCLE using UPGMB clustering method. NJ analysis was performed using MEGA7. The sequences with unverified species assignment and potential contaminants were not considered. NJ tree employed the K2P distance model with pairwise deletion of missing sites and 1000 bootstrap replicates as nodal support. Bootstrap values are shown above the branches (values less than 50% are not shown) using FigTree v1.4.2. Three distinct groups are indicated in yellow [isolates from India, Japan, Thailand, USA, the Dominican Republic, Pakistan, and Taiwan], blue [isolates from Pakistan, India and one isolate each from Bangladesh and the Dominican Republic] and green [isolates from Indonesia]. Three isolates from Pakistan, China, and India branched separately. *Thrips tabaci* (red) was used as an outgroup

ecological niches and environmental conditions. Developmental time for *T. palmi* is reduced with an increase in the temperature resulting in rapid development at 31°C (Yadav and Chang 2012). Similar acceleration effects were also seen in the fecundity and oviposition of *T. palmi*. Although the lower developmental threshold for *T. palmi* was 10.6 °C, they survived cold temperatures between − 2 and − 12.6 °C (Park et al. 2010; 2014). The capacity of *T. palmi* to survive in such a vast range of temperatures may be the reason for their successful establishment throughout Asia, Africa, America, and Oceania. Many physiological changes must take place in *T. palmi* to survive freezing temperatures (Park et al. 2014). One of the most important changes observed was the accumulation of sugar polyols such as glycerol and mannitol which are known cryoprotectants. Cold-exposed *T. palmi* showed about 210-fold increase in trehalose, another cryoprotectant. Accumulation of mannose may support the integrity of proteins and lipid membranes in extreme temperatures (Park et al. 2014). Increased trehalose levels suggest upregulation of trehalose phosphate synthase and trehalose phosphate phosphatase, the genes involved in trehalose biosynthesis (Thompson 2003). Nevertheless, the

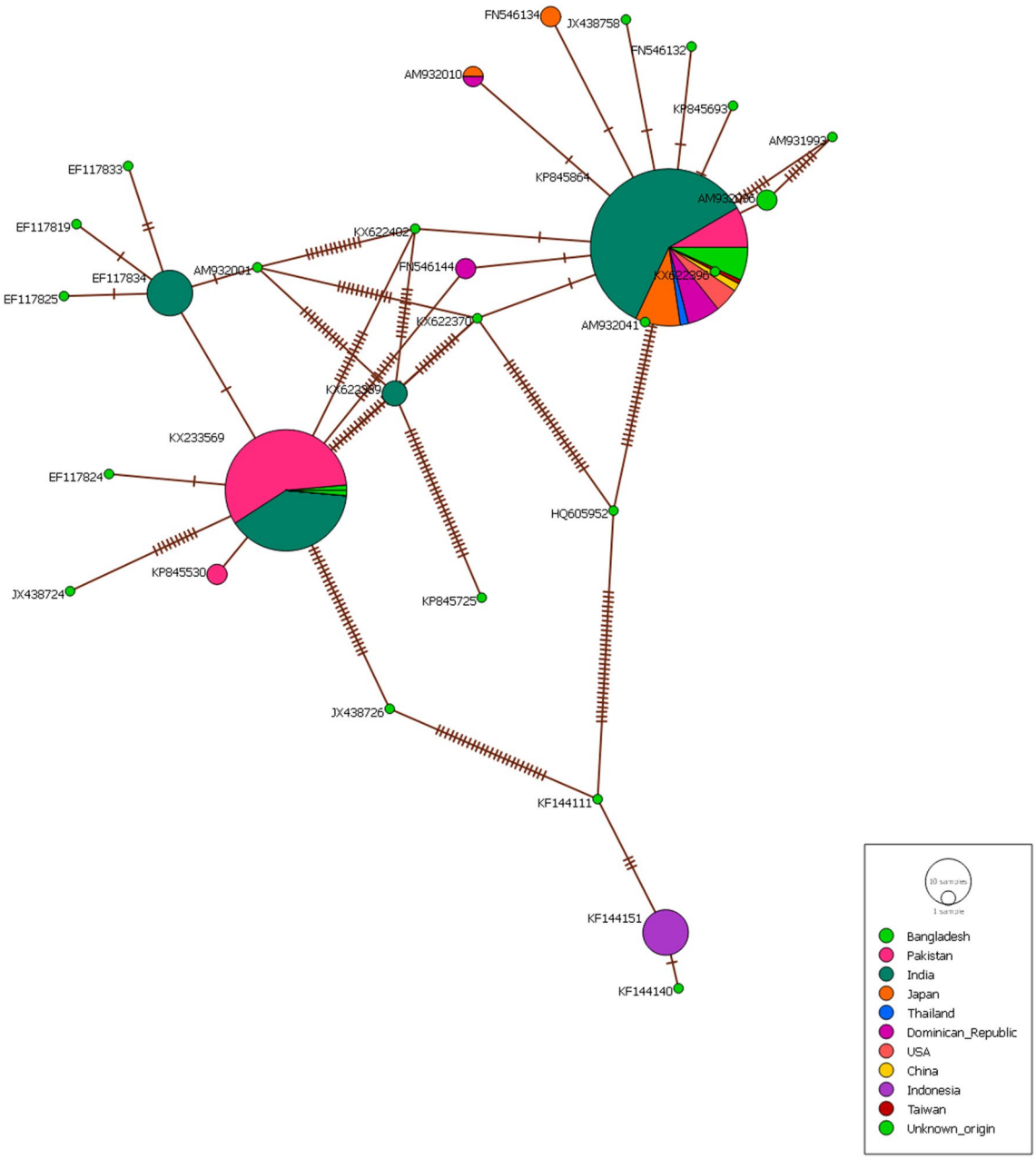

Fig. 2 Haplotype network of *Thrips palmi* based on cytochrome c oxidase I sequences using DnaSP6. A minimum spanning network was constructed using PopART 1.7. Sequences with unverified species assignment and potential contaminants were not considered in the analyses. The circle size is proportional to the frequency of haplotypes. The hatch marks on the lines represent the number of nucleotide substitutions between linked haplotypes. Different pie colors in the circle represent the number and origin of isolates, as shown in the inset box

detailed mechanisms behind the cold-induced upregulation of these genes need to be investigated further. Recently, in *F. occidentalis*, the expression of genes for various heat-shock proteins including HSP90, HSP28.9, HSC704, and HSC705 was found to be upregulated, post-cold exposure, indicating their probable role in thermal adaptation (Wang et al. 2014; Lu et al. 2016; Qin et al. 2018). Heat-shock proteins are also likely involved in cold hardiness of *T. palmi*.

Hitherto, *T. palmi* was considered to be restricted to Asian countries. But increased international travel and commerce, change in human demography, and environment have led to the successful introduction of *T. palmi* throughout the world. Its wide thermal adaptability, especially the capacity to withstand freezing temperatures, helps it to establish in temperate and cold climates in addition to the tropics and subtropics. The available genomic data suggest a role for

trehalose phosphate synthase and different heat-shock proteins in cold tolerance. The detailed mechanism of this abiotic stress response in *T. palmi* warrants future study.

Genetics of insecticide resistance in *T. palmi*

Use of chemical insecticides is the most common option for thrips management in agriculture. However, many widely used insecticides are ineffective against *T. palmi* because of the fast development of insecticide resistance. *T. palmi* has developed resistance to several products of organochlorine, organophosphate, and synthetic pyrethroid including recent chemistries like neonicotinoids and spinosyn (Rajulu and Gowri 1988; Toda and Morishita 2009; Tsukahara et al. 2003).

Pyrethroids are organic axonic excitotoxins similar to the natural pyrethrins (Soderlund et al. 2002). The active molecule binds to the voltage-gated sodium channels in the axons keeping them in an open state, which results in permanent depolarization of neurons, and paralysis of the insects (Soderlund et al. 2002). Many insects have developed resistance against pyrethroids. The most common mechanism of resistance is nerve insensitivity due to mutations in the voltage-gated sodium channel. Mutations M918T in IIS4-IIS5 domains, T929I in IIS5 domain, and L1014F in IIS6 domain have resulted in pyrethroid resistance (Miyazaki et al. 1996; Williamson et al. 1996; Schuler et al. 1998; Tsukahara et al. 2003). Cytochrome P450 (CYP450)-mediated detoxification of pyrethroids was also observed in some insects (Scott 1999). Among the thrips species, *F. occidentalis* demonstrated resistance due to L1014F and T929C mutations in the sodium channel (Forcioli et al. 2002). M918T and L1014F mutations were observed in *Thrips tabaci* (Toda and Morishita 2009). *T. palmi* has developed resistance against cypermethrin because of mutations M843I, A1231D, and T945I in the sodium channel. CYP450 s were also involved in detoxification of cypermethrin in *T. palmi* (Bao and Sonoda 2012).

New chemistries with novel mode-of-action have been introduced to combat the development of insecticide resistance. The first neonicotinoid was introduced during the mid-80s. Imidacloprid, one of the most widely used neonicotinoids, binds to nicotinic acetylcholine receptors (nAChRs) blocking the nicotinergic neuronal pathway. This ultimately prevents transmission of impulses between nerves through acetylcholine resulting in insect paralysis and ultimately death (Buckingham et al. 1997). The nAChR consists of five subunits, each with four transmembrane domains and one extracellular domain (Grutter and Changeux 2001). Imidacloprid-resistant *Nilaparvata lugens*, *Aphis gossypii*, and *Myzus persicae* showed a single point mutation Y151S in the agonist binding domain of the α-subunit or R81T in the β1-subunit loop D of nAChR (Liu et al. 2005; Millar and Denholm 2007; Bass et al. 2011; Koo et al. 2014). In *T. palmi*, imidacloprid resistance was not due to these mutations; instead it was a result of CYP450-mediated detoxification (Bao et al. 2015). Some non-specific esterases may also aid the detoxification of imidacloprid in *T. palmi* (Bao et al. 2015). Enzymes like CYP6G1, CYP6CM1vQ, CYP6ER1, and CYP6AY1 were shown to be involved in imidacloprid metabolism in various insects (Daborn et al. 2001; Roditakis et al. 2011; Bao et al. 2016). Further investigation on the probable role of such enzymes in *T. palmi* would help to better understand the mechanism.

Another novel mode-of-action insecticide which targets the nAChR is Spinosad. Spinosad binds to the insect's central nervous system leading to neuromuscular fatigue, causing paralysis, and ultimately death (Salgado 1998). Spinosad also has secondary effects as a γ-aminobutyric acid neurotransmitter agonist resulting in hyper-excitation of insects leading to death (Watson 2001). Resistance against Spinosad was found to be linked to the mis-splicing of nAChR α6 subunit transcripts resulting in a truncated protein or CYP450-mediated detoxification (Scott 1998; Wang et al. 2009; Baxter et al. 2010; Hsu et al. 2012). In case of *F. occidentalis*, a G275E mutation was identified as resulting in Spinosad resistance (Puinean et al. 2013). The G275E mutation in the nAChR α6 subunit of *T. palmi* also resulted in reduced sensitivity of the receptor to Spinosad. The resistance was further strengthened by CYP450-mediated detoxification of this insecticide (Bao et al. 2014). Apart from target insensitivity and detoxification, some non-specific esterases may also contribute to Spinosad resistance (Bao et al. 2014). In *F. occidentalis*, Spinosad resistance was inherited as an incompletely dominant trait (Zhang et al. 2008). Whether a similar inheritance pattern occurs in *T. palmi* needs to be studied. Development of insecticide resistance to some of the most widely used insecticides including new chemistries makes management of *T. palmi* a very difficult task.

T. palmi genes involved in virus transmission

Several thrips species are vectors of plant viruses classified in the genera *Orthotospovirus*, *Ilarvirus*, *Carmovirus*, *Sobemovirus*, and *Machlomovirus* (Jones 2005). *T. palmi* is known to transmit eight tospoviruses and one ilarvirus (Table 2). The effects of the tospoviruses (genus *Orthotospovirus*, family *Tospoviridae*, order *Bunyavirales*; Abudurexiti et al. 2019) GBNV, WBNV, and watermelon silver mottle virus (WSMoV) on *T. palmi* have been documented recently. It was observed that the survivability and developmental period of GBNV-, WBNV- and WSMoV-exposed *T. palmi* was shortened compared to non-exposed thrips (Chen et al. 2014; Daimei et al. 2017; Ghosh et al. 2019). The exact mechanism of this virus-vector relationship is

Table 2 Viruses transmitted by *Thrips palmi*

Virus name (abbreviation)	Host plant species	References
Tospoviruses		
Calla lily chlorotic spot virus (CCSV)	*Zantedeschia* sp.	Chen et al. (2005)
Capsicum chlorosis virus (CaCV)	*Capsicum annuum*	McMichael et al. (2002)
Groundnut bud necrosis virus (GBNV)	*Arachis* sp., *Solanum lycopersicum*, *Solanum tuberosum*, *Allium cepa*, *Amaranthus* sp., *Calotropis gigantean*, *Commelina benghalensis*, *Colocasia esculenta*, *Corchorus* sp., *Cucumis sativus*, *Eclipta alba*, *Glycine max*, *Phaseolus vulgaris*, *Physalis minima*, *Pisum sativum*, *Sesamum indicum*, *Vigna* sp.	Reddy et al. (1992), https://gd.eppo.int
Melon yellow spot virus (MYSV)	*Citrullus lanatus*, *Cucumis melo*, *Cucumis sativus*, *Momordica charantia*	Kato et al. (2000), https://gd.eppo.int
Tomato necrotic ringspot virus (TNRV)	*Capsicum annuum*, *Solanum lycopersicum*	Seepiban et al. (2011), Puangmalai et al. (2013)
Tomato spotted wilt virus (TSWV)	*Arachis hypogaea*, *Capsicum annuum*, *Gerbera jamesonii*, *Lactuca sativa*, *Nicotiana tabacum*, *Solanum lycopersicum*	Sherwood et al. (2003), https://gd.eppo.int
Watermelon silver mottle virus (WSMoV)	*Citrullus lanatus*, *Cucumis sativus*, *Solanum lycopersicum*	Yeh and Chang (1995)
Watermelon bud necrosis virus (WBNV)	*Citrullus lanatus*	Singh and Krishnareddy (1996)
Ilarviruses		
Tobacco streak virus (TSV)	*Allium cepa*, *Arachis hypogaea*, *Cajanus cajan*, *Cucurbita pepo*, *Glycine max*, *Helianthus annuus*, *Jasminum sambac*, *Lablab purpureus*, *Macrotyloma uniflorum*, *Nicotiana tabacum*, *Ricinus communis*, *Solanum tuberosum*, *Vaccinium macrocarpon*	Ravi et al. (2001), http://www.dpvweb.net

yet to be investigated. The insect cellular receptors and entry mechanisms of several vertebrate bunyaviruses have been studied comprehensively. The host receptor proteins such as C-type lectin, myosin, nucleolin, integrins have been shown to interact with viral glycoproteins (Albornoz et al. 2016). Similar C-type lectin and myosin genes have been recognized in transcriptomes of *T. palmi* (Jagdale and Ghosh 2019), but a tospovirus receptor has not yet been identified. Recently, a set of differentially expressed genes of *F. occidentalis* in response to tomato spotted wilt virus (TSWV; genus *Orthotospovirus*) infection have been identified. Genes including mitochondrial ATP synthase α subunit, vacuolar ATP synthase E subunit, clathrin, adaptor protein, and enolase were found associated with TSWV transmission (Badillo-Vargas et al. 2012; Zhang et al. 2013; Schneweis et al. 2017), suggesting clathrin-mediated endocytosis (CME) of TSWV in *F. occidentalis*. Based on the sequence similarity with *Drosophila melanogaster*, transcripts of all these genes are present in *T. palmi* transcriptomes. Molecular modeling and docking analysis of the respective *T. palmi* proteins with GBNV G_N and G_C predicted protein–protein interactions in silico (Jagdale and Ghosh 2019). The results indicate that C-type lectin is a strong candidate for the cellular receptor in *T. palmi* with which GBNV-G_N is thought to interact to attach to midgut cells and then to get internalized by a process resembling CME. Further, host signal peptidase, signal peptide peptidase, and cathepsin have been reported to be involved in glycoprotein maturation of vertebrate-infecting bunyaviruses (Löber et al. 2001; Hofmann et al. 2013). Analysis of the precursor glycoprotein sequences of GBNV and WBNV using SignalP software (Petersen et al. 2011) identified predicted glycosylation and signal peptidase cleavage sites (Fig. 3). The proposed role of these peptidases and cathepsin in viral glycoprotein maturation in *T. palmi* is yet to be experimentally examined.

Recently, the first annotated transcriptome in the genus *Thrips* was assembled, significantly enriching available genetic information. Transcriptome-wide responses of adult *T. palmi* to infection by capsicum chlorosis virus (CaCV; genus *Tospovirus*) were determined, and 1,389 differentially expressed (DE) transcripts were identified with similar numbers up- and down-regulated in virus-exposed compared to non-exposed thrips (Widana Gamage et al. 2018). Transcripts upregulated in CaCV-exposed *T. palmi* included genes associated with innate immune responses (lysosome activity and melanisation), salivary glands (feeding and digestion), and fitness and fecundity (vitellogenin). Upregulated genes involved in oral and extra-oral digestion of proteins, lipids, and cell wall may indirectly enhance virus transmission or may be involved in host defenses. The

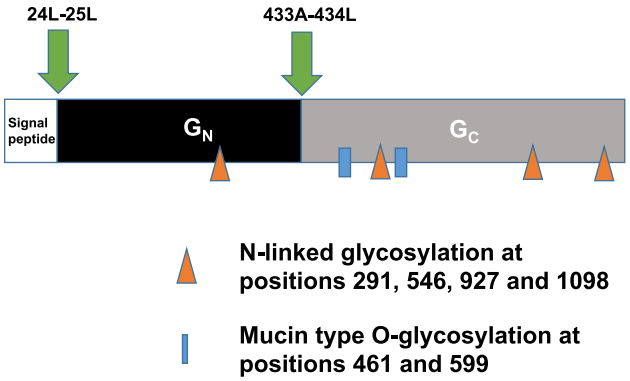

Fig. 3 Schematic representation of G_N and G_C precursor protein of groundnut bud necrosis virus. The green arrows mark the predicted signal peptidase cleavage sites. The precursor protein size is 1121 amino acids. The signal peptide is cleaved between 24 and 25 amino acids. The cleavage between G_N and G_C is at 434–434 amino acids. The orange triangle marks the N-linked glycosylation at 291, 546, 927, and 1098 amino acids. Predicted mucin type O-glycosylation sites at 461 and 599 amino acids are indicated by blue blocks. The diagram was developed based on SignalP 4.1 server output. The glycosylation sites were predicted using NetNGlyc 1.0 and NetOGlyc 4.0 servers

majority of *T. palmi* DE transcripts appeared to be species-specific, but some molecular responses to tospovirus infection were conserved among different thrips species (Widana Gamage et al. 2018). Transcripts associated with thrips feeding and fecundity may be good candidate targets for thrips and tospovirus management.

The molecular mechanisms involved in the acquisition and transmission of tospoviruses by *F. occidentalis* are well-studied, but isolation of the proposed gut receptor for the viral surface glycoprotein has not yet been achieved. Mechanisms involved in virus uptake and replication, protein–protein interactions, and intercellular movement in *T. palmi* also need to be explored. Successful utilization of methods like immunofluorescence confocal laser scanning microscopy to identify a neurotropic route for the rhabdovirus maize mosaic virus in its planthopper vector may also be useful for examining *T. palmi*-tospovirus interactions at the cellular level (Ammar and Hogenhout 2008). Use of three-dimensional imaging techniques like correlative microscopy may be worth exploring to comprehend viral entry, movement, and propagation.

Other molecular tools to study the genetics of *T. palmi*

With the advent of high throughput sequencing, 'omics' studies have become important tools in understanding functional biology. Among the thrips, *F. occidentalis* is the best studied because of its predominance and global economic importance. The differential transcriptomics and proteomics of *F. occidentalis* in respect to TSWV infection revealed the roles of several thrips genes and metabolic pathways during viral infection. Such omics-based studies have only recently started to emerge for *T. palmi*. A study describing the miRNAome of *T. palmi* has been carried out recently (Rebijith et al. 2016). This is the first study describing the microRNA data in a thysanopteran insect. MiRNAs are non-coding RNAs that regulate gene expression and play an important role in cellular and developmental processes (Ambros 2004). In *T. palmi*, 67 miRNAs belonging to 54 families were reported. miR-281 was observed to be most highly expressed which regulates the ecdysone receptor isoform B expression necessary for development and metamorphosis. Another miRNA, miR-750 targets *ultraspiracle*, a gene involved in hormone signaling, immunity, and stress response (Jones and Sharp 1997). Apart from these, roles of many other miRNAs have been described (Rebijith et al. 2016) which could in theory be utilized for developing novel pest management strategies based on gene silencing.

Concluding remarks

Since its first report almost 90 years ago, *T. palmi* remains one of the most important crop pests. Their minute size, wide geographical distribution, large host range, thermal adaptability, and resistance to insecticides make them a worldwide threat. In addition, the capability of *T. palmi* to transmit tospoviruses and ilarviruses has aggravated the field situation. With advancements in molecular biology in the past few years, the genome data of *T. palmi* and its interactions with the viruses it transmits have been significantly boosted. Availability of these genetic data is increasingly being exploited to better understand many unresolved ambiguities related to biology, virus transmission, systematics, behavior, physiology, and evolution of *T. palmi*. The close interrelationship of *T. palmi* with tospoviruses may be targeted to restrict virus spread (Ghosh et al. 2017). Furthermore, transcriptome and miRNA profiling of *T. palmi* could potentially be utilized to develop RNA-silencing-based control strategies for thrips populations (Rebijith et al. 2016). More consolidated approaches in genomics, transcriptomics, and proteomics of *T. palmi* and comparative analyses with genomics of other thrips species should be undertaken in order to shed more light on functional biology of this important plant pest.

Author contributions

AG conceived and designed the review. SJ and AG read through the related publications and wrote the draft manuscript. BYB, RKJ, RGD critically reviewed the manuscript and suggested edits; RGD contributed new information,

redrafted the manuscript, assisted with English language editing and communicated with the editorial office. All authors read and approved the manuscript.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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