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Reproductive biology and behaviour in the onion thrips cryptic species complex

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1. Background, objectives

Thrips (Thysanoptera HALIDAY 1836) are one of the smallest insects. For most people, they usually remain unnoticed, yet many species are significant pests (Lewis 1973, Lewis 1997). However, many aspects of the biology of thrips is unknown (Mound 2005), including details regarding their reproductive biology.

Besides their direct feeding damage, numerous species of thrips are also important vectors of *Orthotospovirus* species (Ullman et al. 1997, Riley et al. 2011). Orthotospoviruses can be transmitted mechanically, however, under natural conditions they are spread primarily by thrips in a persistent-propagative manner (Whitfield et al. 2005, Rotenberg et al. 2015). The type species of the genus *Orthotospovirus* is *O. tomatomaculae* – formerly and better known as *Tomato spotted wilt orthotospovirus* (TSWV) – a highly polyphagous species, which is one the most important plant pathogens worldwide (Whitfield et al. 2005, Pappu et al. 2009, Scholthof et al. 2011). In order to transmit TSWV, thrips must acquire it as young larvae (van de Wetering et al. 1996, Chatzivassiliou et al. 2002), therefore, it is crucial to know, whether adult females prefer to oviposit on infected plants.

The onion thrips (*Thrips tabaci* LINDEMAN) is one of the most important pest species in the order Thysanoptera; being a significant pest due to its direct damage on numerous crops, and also a vector of TSWV (Jenser and Szénási 2004, Riley et al. 2011, Diaz-Montano et al. 2011). However, neither the reproductive behaviour of this pest, nor the effect of TSWV on onion thrips are known in details.

Moreover, studies from recent years showed that onion thrips is rather a cryptic species complex with distinct lineages differing from each other in their genetics and ecological traits (Brunner et al. 2004, Toda and Murai 2007, Farkas et al. 2020). Currently, three lineages of onion thrips are known (based on differences in the sequences of their mitochondrial COI region): the T (tobaccoassociated), and the L1 and L2 (leek-associated) lineages, collected originally from tobacco and leek, respectively (Brunner et al. 2004).

Studies from the past years showed that the T and L1 lineages are reproducing by arrhenotoky, and the T lineage by thelytoky (Toda and Murai 2007, Farkas et al. 2020). Thelytokous females are able to produce female progeny without mating and insemination, while arrhenotokous females are only able to give birth to daughters after mating; from their unfertilized eggs only males hatch (Moritz 1997, Kumm and Moritz 2008, Vershinina and Kuznetsova 2016).

Among these lineages both L1 and L2 are polyphagous, sharing numerous host plants, however the L2 has an even broader host range and distribution (Loredo Varela és Fail 2022). Both of these lineages can be a pest of onion and cabbage, but fail to survive on tobacco (Chatzivassiliou et al.. 2002, Li et al. 2014, Fail 2016). The T lineage has the narrowest host range, occurring almost exclusively on tobacco and on some weeds (Zawirska 1976, Loredo Varela és Fail 2022).

Considering the aforementioned gaps in our knowledge regarding the biology of onion thrips, we focused our research towards areas related to the reproductive biology of this pest. We aimed to reveal and understand ecological relationships not only among the lineages, but also between onion thrips and TSWV.

Our main objectives were:

1. To investigate the possibility of reproductive isolation among the lineages in the onion thrips cryptic species complex.
2. To observe the mating behaviour of all the known lineages.
3. To analyse the effect of TSWV infection on the oviposition preference of onion thrips.
4. To investigate the effect of TSWV infection on the sex ratio of the T lineage of onion thrips.

2. Materials and Methods

In order to have thrips with a known pedigree, isofemale lines were established. In most cases, randomly selected individuals from our stock cultures were used for starting these lines, but some females collected directly from the open field were also used. Stock colonies with all the three known onion thrips lineages (T, L1 and L2) were established in 2013–2014 by colleagues working at the Department of Entomology then (Farkas et al. 2020), and maintained ever since. Both the selected females and their progeny were placed individually into microcentrifuge tubes (2 ml), therefore thrips with a known age and pedigree were obtained and used for our experiments. All of the isofemale lines used in these studies were identified to onion thrips lineage level based on the molecular method of Farkas et al.(2020).

No-choice cross-mating experiments were carried out among the three known onion thrips lineages in order to observe their mating behaviour and to test for the possibility of reproductive isolation. For each replication a virgin male and virgin female, 2–7 days after adult eclosion, were placed together in a small arena, made from the cap of a 2 ml microcentrifuge tube and covered with a glass cover slip. The behaviour of the thrips were monitored and recorded for 10 minutes with a digital camera mounted on a stereomicroscope. The existence of two arrhenotokous (T and L1) lineages and one thelytokous (L2) lineage in the species complex resulted in six possible combinations (pairings) of males and females. Pairings with one thrips originated from an L, and the other from the T lineage were called cross pairings, while the remaining three combinations were considered as controls.

The effect of TSWV on the oviposition preference of onion thrips females were investigated with the T and L2 lineages. For these experiments small dishes with a diameter of 4 cm made of translucent plastic with a tight sealing lid were used. Two leaf disks (approximately 11 mm in diameter) were placed into each dish arranged equidistant from the centre. For our choice assays pepper and tobacco plants were used, with one leaf disk punched out from a leaf of a TSWV infected plant, and the other from a leaf of a control (mock-inoculated) plant of the same species. No-choice assays were conducted only with pepper leaf disks. In these assays either both of the leaf disks provided to thrips females were of a TSWV infected plant, or both of them were of a control plant. One onion thrips female was introduced into every dishes, and left to oviposit for 48 hours. To investigate the settling behaviour of the females, 24 and 48 hours after the start of each replicate the residence of the females were also recorded.

After 48 hours the females were removed from the dishes and the number of eggs oviposited into each leaf disks were counted and recorded. For the oviposition preference tests only mated females were used from the T lineage, therefore it was possible to investigate the effect of TSWV infection on the sex ratio of thrips. For this, after the removal of the female the leaf disks were kept separately until the eggs oviposited into the leaf tissue hatched. Hatched larvae (F_2 generation) were then killed in ethanol, slide mounted and their sex were determined.

3. Results and discussion

In total, 188 isofemale lines were identified molecularly. Based on their mtCOI region, all of the lines proved to belong to the lineage as expected, except one. This one isofemale line originated from our L1 culture, and indeed was found to be arrhenotokous, as all the offspring of the originally isolated female that reached adulthood were males, however, the mtCOI of the line was characteristic of the thelytokous lineage. Therefore, we reported onion thrips with arrhenotokous reproduction, but with an mtCOI characteristic of the L2 lineage for the first time from Europe. We assume, that these lines are perhaps a result of hybridization between the L1 and L2 lineages, but it needs further investigation.

3.1. Results of the mating experiments

This was the first comprehensive study of the reproductive behaviour of onion thrips that involved all three known lineages from this cryptic species complex. We concluded – based on observations of 67 mating control pairs – that there were no marked differences among the lineages regarding their behaviour and that the copulation behaviour of onion thrips lineages resembles that of other thripid species as well (Terry and Schneider 1993, Milne et al. 2007, Rafter and Walter 2013, Krueger et al. 2017, Akinyemi és Kirk 2019, Akinyemi et al. 2021).

In our experiments the control pairs usually mated in their first interaction event. In the interaction events that led to successful mating in these control pairings, usually males approached the females. After approaching, the male sensed the female and contacted her physically before male mounting followed. Upon mounting the female, the male bent his abdomen beneath that of the female. Next, the male inserted his aedeagus into the female genitalia and copulation started.

During copulation, the females were usually calm, but some types of rejection behaviour (arching and/or flipping their abdomen up and down), occurred frequently, most often in the L2♀ + L1♂ combinations. This result, together with other observed small differences between the L1♀ + L1♂ and L2♀ + L1♂ pairings indicated some form of loss of function in the thelytokous females' sexual traits.

Our results showed no significant differences among the control pairings for the duration of precopulation. However, the duration of copulation was significantly different, and pairwise comparisons revealed that all control pairings differed from each other ($p < 0{,}01$), with the mating of L1♀ + L1♂ pairs being the shortest (140 seconds), and T♀ + T♂ the longest (176 seconds).

After mating, at the beginning of the upcoming interaction events, mated thrips seemed to behave the same way as virgin individuals did. However, after copulation there was a significant increase in the ratio of interaction events with male rejection behaviour ($p < 0.001$). During male rejection behaviour, males started to mount the females, or even climbed successfully onto the females' back, then stopped and reversed the movement, therefore discontinued the mating sequence, stopped trying to mate with the females, and climbed down from their backs.

This observation showed that though males often started to try and copulate again with the females they have mated with before, they eventually sensed something that forced them to avoid proceeding further in the mating sequence. We believe that this strongly indicated the presence of an anti-aphrodisiac pheromone, which acted primarily upon contact, and is presumably produced by the males and applied to the females during copulation. In the order Thysanoptera such substances are only identified so far in *Echinothrips americanus* MORGAN (Krueger et al. 2016), but our findings and hypothesis also match the findings of Akinyemi and Kirk (2019), who observed that experienced (mated) western flower thrips [*Frankliniella occidentalis* (PERGANDE)] males mated with virgin females, but avoided copulating with mated females.

During our 10-minute-long standard observation period, no copulations occurred in L1♀ + T♂ and T♀ + L1♂ combinations and only two matings were recorded between L2♀ + T♂ pairings (Table 1). However, the durations of these copulations were notably shorter: 70 and 71 seconds. This indicated that these two T lineage onion thrips males assessed L2 females to be of a high enough quality to copulate with them, but even these males substantially reduced the duration of their mating, which is regarded as a type of cryptic male mate choice.

Divergence among cross and control pairings in our experiments appeared to start only after interaction, and became even stronger after male mounting, indicating the presence of cues acting only upon contact, such as cuticular-hydrocarbons (CHCs), which seems to be widespread in arthropods (Howard and Blomquist 2005, Jungwirth et al. 2021). The difference between the control and cross pairings was significant after physical contact, when T males avoided mounting L1 or L2 females, and L1 males avoided mounting T females ($p < 0.05$; Table 1). The divergence continued in the next phase, as the difference was also statistically significant between cross and control pairings in the frequency of pairs with males not only mounting the females but also bending their abdomens beneath those of the females ($p < 0.05$).

Taking all these together we concluded, that the L and T lineages in the onion thrips species complex should be considered as distinct species, since reproductive isolation is so strong among them even under laboratory conditions, which would certainly mean complete isolation under natural conditions.

Table 1 The percentage of pairs that completed each step in the mating behaviour sequence as a proportion of those (n) that completed the previous step

Step in the mating behaviour sequence	**T♀ + T♂**	**T♀ + L1♂**	**L1♀ + L1♂**	**L1♀ + T♂**	**L2♀ + L1♂**	**L2♀ + T♂**	**p value**
Interaction	57 % (n = 42) *a*	67 % (n = 45) *ab*	76 % (n = 33) *ab*	94 % (n = 32) *b*	78 % (n = 41) *ab*	78 % (n = 41) *ab*	< 0.010
Contact	96 % (n = 24)	97 % (n = 30)	92 % (n = 25)	93 % (n = 30)	88 % (n = 32)	97 % (n = 32)	= 0.720
Male mounting	96 % (n = 23) *b*	17 % (n = 29) *a*	100 % (n = 23) *b*	36 % (n = 28) *a*	93 % (n = 28) *b*	29 % (n = 31) *a*	< 0.001
Bend abdomen	100 % (n = 22) *b*	20 % (n = 5) *a*	100 % (n = 23) *b*	20 % (n = 10) *a*	96 % (n = 26) *b*	22 % (n = 9) *a*	< 0.001
Mating	100 % (n = 22)	0 % (n = 1)	100 % (n = 23)	0 % (n = 2)	88 % (n = 25)	100 % (n = 2)	= 0.103

p values were calculated using Fisher's exact tests for a 6 × 2 contingency table with the frequencies of pairs that did or did not complete a step in the mating behaviour sequence as one factor, and the six different pairings as the other. Exception is "Mating", for which only the control pairings (T♀ + T♂, L1♀ + L1♂, L2♀ + L1♂) were included in the analysis; therefore, p values were calculated using Fisher's exact test for a 3 × 2 contingency table. If the Fisher's exact test gave significant result, Marascuilo's procedure were used for the pairwise comparisons. Different letters in italic within each row across columns show significant deviations between the percentages of different pairs that completed a step in the mating behaviour sequence (Marascuilo's procedure, $p < 0.05$*).*

Our results also showed that onion thrips lineages differ from each other in their level of activity. Most interestingly, we observed that in many cases, one of the individuals from the cross pairings reacted to a contact with the other thrips by running away in excitement, usually with a rapid change in behaviour (escape response). Statistical analysis showed that T lineage onion thrips reacted with an escape response significantly more often than L1 lineage onion thrips, irrespectively of the investigated sex ($p < 0.01$).

3.2. Results of the oviposition preference tests

Our results showed that for the L2 lineage, tobacco proved to be an unsuitable host irrespectively of the status of TSWV infection. In choice assays the average number of eggs on tobacco leaf disks was only 0.73 egg/female, moreover, it seemed that neither the females nor the hatched larvae were able to feed on the leaf disks, therefore larvae died without further development.

In choice assays with pepper leaf disks females from the T onion thrips lineage laid 81,4 % of their eggs into the TSWV infected leaf disks, while females from the L2 lineage chose the infected leaf disks in only 46,6 % of the cases. However, on tobacco plants both lineages preferred the uninfected leaf disks for oviposition. Therefore, the TSWV infection had a strong effect on the oviposition preference of onion thrips females, but the direction of the effect was different on the two host plants (Figure 1).

The total number of eggs oviposited by the females in the no-choice assays on pepper leaf disks were analysed together with the total number of eggs laid in the choice assays on the same plant species. We concluded that the two studied lineages of onion thrips differed from each other significantly ($p < 0.001$). The effect of the treatments was also significant ($p < 0.001$), and the interaction of the lineage*treatment as well ($p < 0.05$). The results showed, that the TSWV infected pepper is a better host for both onion thrips lineages than the uninfected, and that the availability of only one infected leaf disk (choice assays) could increase the fecundity of females to the same level as it was in the no-choice assays, on infected leaf disks only (Figure 2).

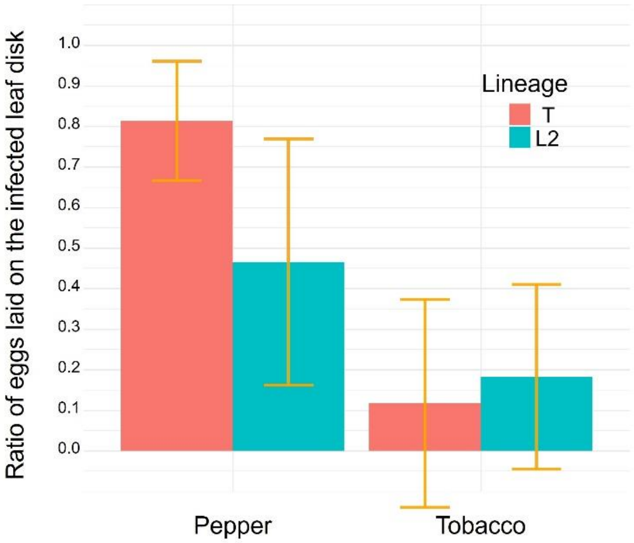

Figure 1 The ratio of eggs laid on the infected leaf disks by onion thrips females from different onion thrips lineages on pepper and on tobacco in choice assays

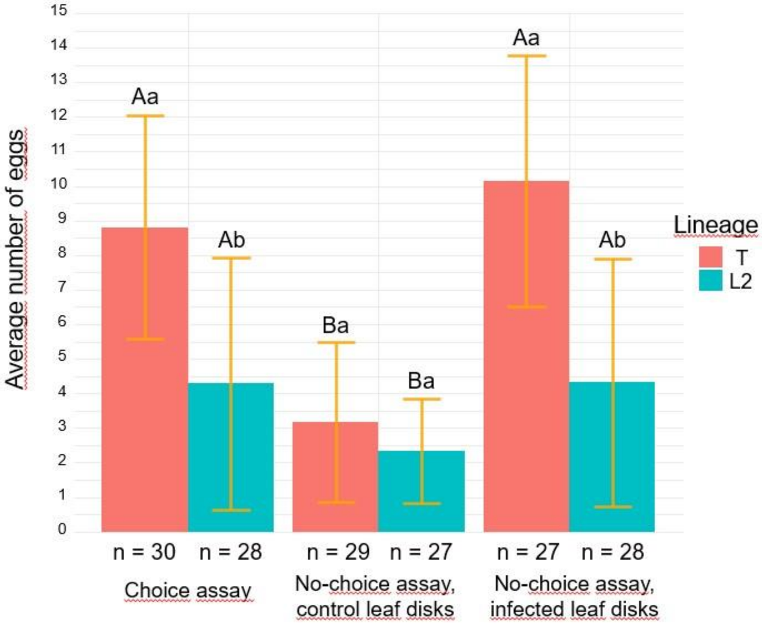

Figure 2 The average number of eggs laid (to the two leaf disks in total in each dish) by females from different onion thrips lineages on pepper leaf disks in different treatments (number of eggs ± SD). Different capital letters show significant differences between treatments within the same lineage, and different small letters between lineages within each treatment ($p < 0.05$).

We concluded, that TSWV infection had a positive indirect effect on pepper leaf disks for both the L2 and T lineages of onion thrips, and this resulted in an increased fecundity. However, based on the total number of eggs laid, for the L2 lineage not even the TSWV infected leaf disks could serve as a good food source, while it could for the T lineage, because the increase in the oviposition rate was substantially higher for the T lineage.

Only mated females were used for our experiments from the T lineage (which reproduces by arrhenotoky), hence we were able to test the effect of TSWV infection on the sex ratio of the progeny (F_2 generation). The ratio of females among the hatched larvae were higher in every comparison on infected leaf disks than on uninfected ones, but the difference was not significant. In choice assays on pepper 83,1 % of the hatched larvae were females on infected, and 79,0 % on uninfected leaf disks. On tobacco 77,0 % and 70,6 % of the hatched larvae were females on infected and uninfected leaf disks, respectively. In the no-choice assays 85,5 % of the progeny were females when only infected pepper leaf tissue were provided to their mothers, but only 77,0 % when two uninfected leaf disks served as food source. We believe, that these results strengthen the hypothesis that TSWV infection had a positive indirect effect on the thrips, since in an arrhenotokous population the higher ratio of females enhance the growth of the population.

4. Conclusions and recommendations

We reported onion thrips with arrhenotokous reproduction, but with an mtCOI characteristic of the thelytokous lineage, for the first time from Europe, however, its occurrence was very rare (only 1 line out of 188). Our assumption that these lines could be a result of hybridization between the L1 and L2 lineages clearly needs further investigation. We recommend to study the genetics of onion thrips lineages in more details, focusing not only on the mitochondrial, but also on the nuclear DNA.

We found that the mating behaviour of onion thrips lineages only differ in the duration of copulation, otherwise they are quite similar to each other, and they also resemble to the mating behaviour of other thripid species, including western flower thrips regarding the duration of copulation. We recommend to investigate the effect of the duration of copulation on the fecundity in more details, since such knowledge is lacking in the order Thysanoptera. We confirmed that onion thrips from the L1 and L2 lineages mate with each other; however, the observed differences pointed to some form of loss of function in the sexual traits of thelytokous females.

Based on the change in the behaviour of males after copulation we concluded, that a so-called anti-aphrodisiac pheromone exists in onion thrips, since experienced males investigated mated females, but did not try to copulate with them again. However, the compounds and the source of this pheromone is unknown, and we can only presume that it is applied to the back of the females by the males. This substance affected the behaviour of thrips strongly, though, therefore further investigation in the future could reveal a repellent substance for the plant protection practice as well.

We also concluded that the T and L lineages of the onion thrips cryptic species complex are reproductively isolated from each other, since in the cross pairings no successful mating was observed among them. Behavioural patterns of control and cross pairs started to differ substantially only after contact, suggesting an important role of contact pheromones in assessing each other as suitable mating partners. Therefore, we highly recommend the investigation of CHCs as contact pheromones in order to verify this theory. We believe that based on the observed reproductive isolation the T and L lineages should be considered as distinct species.

We found that the L2 lineage of onion thrips do not accept tobacco as a host plant irrespectively of the status of TSWV infection of the plant. This strengthen the hypothesis that the L and T lineages represent distinct species, as for the T lineage tobacco is considered as the primary host plant.

We concluded that the TSWV infection has a positive indirect effect on both the T and the L2 lineages, since females were able to lay more eggs when feeding on TSWV infected compared to uninfected pepper leaf disks. We determined that for the T lineage pepper without virus infection is only a poor host, but upon TSWV infection it became a much superior one, as good as tobacco. Females from this lineage also showed a significant preference towards infected plant material, which clearly increase the risk of transmission within pepper fields.

We found that the ratio of females among the progeny of T lineage females were consistently higher in every comparison on infected tissue than on uninfected leaf disks, but the difference was not significant.

As a „side effect" of our experiments we also observed notable differences in the activity of onion thrips lineages. Since we frequently observed in the cross pairings that one of the individuals showed an escape response upon contact with the other thrips, we recommend the investigation of cuticular hydrocarbons and contact pheromones in the onion thrips lineages, as it could yield a substance repellent to thrips.

5. New scientific results

1. Onion thrips individuals with arrhenotokous mode of reproduction, but with a mitochondrial DNA characteristic to thelytokous phylogenetic clade were identified for the first time from Europe.
2. The mating behaviour of all the known onion thrips lineages was reported for the first time.
3. Differences in the behaviour of onion thrips males as a function of meeting with a virgin or a mated female was reported for the first time. Males avoided to copulate with mated females, and their behaviour suggested the role of an anti-aphrodisiac pheromone.
4. It was concluded that the T and L lineages of onion thrips are reproductively isolated from each other, therefore should be considered as distinct species.
5. It was found that though thelytokous (L2) females mate with arrhenotokous (L1) males, rejection behaviour of these females during precopulation were more frequent than in the L1♀ + L1♂ pairs.
6. The effect of TSWV infection on the oviposition behaviour of onion thrips females was reported for the first time, with the conclusion that T lineage females prefer to oviposit on infected pepper plants, however, on the contrary they prefer to lay their eggs on uninfected tobacco plants.
7. It was concluded that the TSWV infected pepper plants are better hosts for both the T and the L2 lineage of onion thrips, based on their higher oviposition rate on infected leaf disks.
8. It was reported that for the L2 lineage of onion thrips the TSWV infected tobacco are not suitable as a host plant.
9. Differences in the activity among onion thrips lineages were determined for the first time.

References

Akinyemi, A. O., & Kirk, W. D. J. (2019). Experienced males recognise and avoid mating with non-virgin females in the western flower thrips. *PLoS ONE*, *14*(10), e0224115. https://doi.org/10.1371/journal.pone.0224115

Akinyemi, A. O., Subramanian, S., Mfuti, D. K., Pope, T. W., Tamiru, A., & Kirk, W. D. J. (2021). Mating behaviour, mate choice and female resistance in the bean flower thrips (*Megalurothrips sjostedti*). *Scientific Reports*, *11*(1), 14504. https://doi.org/10.1038/s41598-021-93891-5

Brunner, P. C., Chatzivassiliou, E. K., Katis, N. I., & Frey, J. E. (2004). Host-associated genetic differentiation in *Thrips tabaci* (Insecta; Thysanoptera), as determined from mtDNA sequence data. *Heredity*, *93*(4), 364–370. https://doi.org/10.1038/sj.hdy.6800512

Chatzivassiliou, E. K., Peters, D., & Katis, N. I. (2002). The Efficiency by Which *Thrips tabaci* Populations Transmit *Tomato spotted wilt virus* Depends on Their Host Preference and Reproductive Strategy. *Phytopathology*, *92*(6), 603–609. https://doi.org/10.1094/PHYTO.2002.92.6.603

Diaz-Montano, J., Fuchs, M., Nault, B. A., Fail, J., & Shelton, A. M. (2011). Onion Thrips (Thysanoptera: Thripidae): A Global Pest of Increasing Concern in Onion. *Journal of Economic Entomology*, *104*(1), 1–13. https://doi.org/10.1603/EC10269

Fail, J. (2016). Speciation in Thrips tabaci Lindeman, 1889 (Thysanoptera): The current state of knowledge and its consequences. *Polish Journal of Entomology*, *85*(1), 93–104. https://doi.org/10.1515/pjen-2016-0004

Farkas, P., György, Zs., Tóth, A., Sojnóczki, A., & Fail, J. (2020). A simple molecular identification method of the Thrips tabaci (Thysanoptera: Thripidae) cryptic species complex. *Bulletin of Entomological Research*, *110*(3), 397–405. https://doi.org/10.1017/S0007485319000762

Howard, R. W., & Blomquist, G. J. (2005). Ecological, Behavioral, and Biochemical Aspects of Insect Hydrocarbons. *Annual Review of Entomology*, *50*(1), 371–393. https://doi.org/10.1146/annurev.ento.50.071803.130359

Jenser, G., & Szénási, Á. (2004). Review of the biology and vector capability of Thrips tabaci Lindeman (Thysanoptera: Thripidae). *Acta Phytopathologica et Entomologica Hungarica*, *39*(1–3), 137–155. https://doi.org/10.1556/APhyt.39.2004.1-3.14

Jungwirth, S., Ruther, J., & Pokorny, T. (2021). Similar Is Not the Same – Mate Recognition in a Parasitoid Wasp. *Frontiers in Ecology and Evolution*, *9*, 646667. https://doi.org/10.3389/fevo.2021.646667

Krueger, S., Jilge, M., Mound, L., & Moritz, G. B. (2017). Reproductive Behavior of Echinothrips americanus (Thysanoptera: Thripidae). *Journal of Insect Science*, *17*(2). https://doi.org/10.1093/jisesa/iex043

Krueger, S., Moritz, G., Lindemann, P., Radisch, D., & Tschuch, G. (2016). Male Pheromones Influence the Mating Behavior of Echinothrips americanus. *Journal of Chemical Ecology*, *42*(4), 294–299. https://doi.org/10.1007/s10886-016-0685-z

Kumm, S., & Moritz, G. (2008). First Detection of Wolbachia in Arrhenotokous Populations of Thrips Species (Thysanoptera: Thripidae and Phlaeothripidae) and Its Role in Reproduction. *Environmental Entomology*, *37*(6), 1422–1428. https://doi.org/10.1603/0046-225X-37.6.1422

Lewis, T. (1973). *Thrips, Their Biology, Ecology and Economic Importance*. Academic Press.

Lewis, T. (1997). Pest Thrips in Perspective. In T. Lewis (Szerk.), *Thrips as Crop Pests* (o. 1–13). CAB International.

Li, X.-W., Fail, J., Wang, P., Feng, J.-N., & Shelton, A. M. (2014). Performance of Arrhenotokous and Thelytokous *Thrips tabaci* (Thysanoptera: Thripidae) on Onion and Cabbage and Its Implications on Evolution and Pest Management. *Journal of Economic Entomology*, *107*(4), 1526–1534. https://doi.org/10.1603/EC14070

Loredo Varela, R. C., & Fail, J. (2022). Host Plant Association and Distribution of the Onion Thrips, Thrips tabaci Cryptic Species Complex. *Insects*, *13*(3), 298. https://doi.org/10.3390/insects13030298

Milne, M., Walter, G. H., & Milne, J. R. (2007). Mating Behavior and Species Status of Host-Associated Populations of the Polyphagous Thrips, Frankliniella schultzei. *Journal of Insect Behavior*, *20*(3), 331–346. https://doi.org/10.1007/s10905-007-9081-4

Moritz, G. (1997). Structure, Growth and Development. In T. Lewis (Szerk.), *Thrips as Crop Pests* (o. 15–63). CAB International.

Mound, L. A. (2005). Thysanoptera: Diversity and Interactions. *Annual Review of Entomology*, *50*(1), 247–269. https://doi.org/10.1146/annurev.ento.49.061802.123318

Pappu, H. R., Jones, R. A. C., & Jain, R. K. (2009). Global status of tospovirus epidemics in diverse cropping systems: Successes achieved and challenges ahead. *Virus Research*, *141*(2), 219–236. https://doi.org/10.1016/j.virusres.2009.01.009

Rafter, M. A., & Walter, G. H. (2013). Mate Recognition in the South African Citrus Thrips Scirtothrips aurantii (Faure) and Cross-Mating Tests with Populations from Australia and South Africa. *Journal of Insect Behavior*, *26*(6), 780–795. https://doi.org/10.1007/s10905-013-9391-7

Riley, D. G., Joseph, S. V., Srinivasan, R., & Diffie, S. (2011). Thrips Vectors of Tospoviruses. *Journal of Integrated Pest Management*, *2*(1), I1–I10. https://doi.org/10.1603/IPM10020

Rotenberg, D., Jacobson, A. L., Schneweis, D. J., & Whitfield, A. E. (2015). Thrips transmission of tospoviruses. *Current Opinion in Virology*, *15*, 80–89. https://doi.org/10.1016/j.coviro.2015.08.003

Scholthof, K. G., Adkins, S., Czosnek, H., Palukaitis, P., Jacquot, E., Hohn, T., Hohn, B., Saunders, K., Candresse, T., Ahlquist, P. és mtsai (2011). Top 10 plant viruses in molecular plant pathology. *Molecular Plant Pathology*, *12*(9), 938–954. https://doi.org/10.1111/j.1364-3703.2011.00752.x

Terry, I., & Schneider, M. (1993). Copulatory behavior and mating frequency of the western flower thrips, Frankliniella occidentalis (Insecta: Thysanoptera). (Advances in Thysanopterology). *Journal of Pure and Applied Zoology*, *4*, 339–354.

Toda, S., & Murai, T. (2007). Phylogenetic analysis based on mitochondrial COI gene sequences in Thrips tabaci Lindeman (Thysanoptera: Thripidae) in relation to reproductive forms and geographic distribution. *Applied Entomology and Zoology*, *42*(2), 309–316. https://doi.org/10.1303/aez.2007.309

Ullman, D. E., Sherwood, J. L., & German, T. L. (1997). Thrips as Vectors of Plant Pathogens. In *Thrips as Crop Pests* (o. 539–565). CAB International.

van de Wetering, F., Goldbach, R., & Peters, D. (1996). Tomato spotted wilt tospovirus ingestion by first instar larvae of Frankliniella occidentalis is a prerequisite for transmission. *Phytopathology*, *86*, 900–905.

Vershinina, A. O., & Kuznetsova, V. G. (2016). Parthenogenesis in Hexapoda: Entognatha and non-holometabolous insects. *Journal of Zoological Systematics and Evolutionary Research*, *54*(4), 257–268. https://doi.org/10.1111/jzs.12141

Whitfield, A. E., Ullman, D. E., & German, T. L. (2005). Tospovirus-Thrips Interactions. *Annual Review of Phytopathology*, *43*(1), 459–489. https://doi.org/10.1146/annurev.phyto.43.040204.140017

Zawirska, I. (1976). Untersuchungen über zwei biologische Typen von Thrips tabaci Lind. (Thysanoptera: Thripidae) in der VR Polen. *Archiv für Phytopathologie und Pflanzenschutz*, *12*(6), 411–422.

6. List of publications

Publications related to the topic of the thesis:

Publications in peer-reviewed scientific journals with IF:

- **Király, K. D.**, Ladányi, M., Fail, J. (2022): Reproductive Isolation in the Cryptic Species Complex of a Key Pest: Analysis of Mating and Rejection Behaviour of Onion Thrips (*Thrips tabaci* Lindeman). *Biology*, 11: 396. (Q1)
- Subr, Z. W., **Király, K. D.**, Fail, J., Almási, A., Salánki, K., Fedor, P. (2019): Efficient RT-PCR tool for tomato spotted wilt virus detection in its vectors *Thrips tabaci* and *Frankliniella occidentalis. Acta virologica*, 63: 341 – 343.

Publications in peer-reviewed scientific journals without IF:

- **Király K. D.**, Farkas P., Fail J. (2018): A nyugati virágtripsz (*Frankliniella occidentalis* /Pergande, 1895/) [Western flower thrips (*Frankliniella occidentalis* (Pergande, 1895))]. *Növényvédelem,* 54: 377-398. [in Hungarian, with English summary]
- **Király K. D.**, Reiter D., Farkas P., Sojnóczki A., Fail J. (2017): Előzetes adatok a telitok dohánytripsz gazdanövénykőréhez. [Preliminary results about the host range of the thelytokous onion thrips.] *Növényvédelem,* 53: 49-58. [in Hungarian, with English summary]

Abstracts of conferences:

- **Király K. D.**, Ladányi M., Fail J. (2021): A dohánytripsz párosodási viselkedése. *67. Növényvédelmi Tudományos Napok,* p. 16.
- Szántó F. V., **Király K. D.,** Almási A., Salánki K., Fail J. (2020): A TSWV fertőzöttség hatása a dohánytripsz élettábla paramétereire. *66. Növényvédelmi Tudományos Napok*, p. 29. (Budapest, 2020. február 18-19.)
- **Király K. D.**, Almási A., Salánki K., Fail J. (2019): A paradicsom bronzfoltosság vírus (TSWV) fertőzöttség hatásának vizsgálata a dohánytripsz gazdanövény preferenciájára. *65. Növényvédelmi Tudományos Napok*, p. 26. (Budapest, 2019. február 19-20.)
- Farkas P., Gilbert B., Sojnóczki A., **Király K.**, Pénzes B., Fail J. (2018): A gazdanövény hatása a dohány specialista *Thrips tabaci* Lind. ivararányára. *64. Növényvédelmi Tudományos Napok*, p. 24. (Budapest, 2018. február 20-21.)
- **Király, K. D.** and Fail, J. (2017): How do tospoviruses affect their thrips vectors? A review about the current knowledge. *5th Symposium on Palearctic*

Thysanoptera: Book of abstracts, p. 26. (Cracow, Poland, September 26-29. 2017.)

Other published articles:

- **Király K. D.**, Fail J. (2021): A tripszek feromonjairól és azok (lehetséges) növényvédelmi szerepéről. *Agrofórum*, 32: 72-74.
- **Király K. D.**, Farkas P., Fail J. (2017): A nyugati virágtripsz (*Frankliniella occidentalis*) (Inváziós kártevők (II./14.). *Agrofórum*, 28: 40-46.