

**Speciation in *Thrips tabaci* LINDEMAN, 1889 (Thysanoptera):
the current state of knowledge and its consequences***

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ABSTRACT. Based on DNA sequences of the mitochondrial COI gene, *Thrips tabaci* has been divided into three lineages: a tobacco-associated (T) and two leek-associated types (L1, L2). It is believed that the arrhenotokous leek-associated type (L1) is the ancient form of *T. tabaci* and that the T type diverged from it and adapted to solanaceous host plants. The third lineage of *T. tabaci*, the so-called thelytokous leek-associated type (L2) and the L1 form share many host plants. According to a recent study, the L2 form of *T. tabaci* could outcompete the L1 type on cabbage plants; it might therefore be more accurate to identify it as the thelytokous cabbage-associated type.

KEY WORDS: *Thrips tabaci*, speciation, arrhenotoky, thelytoky.

INTRODUCTION

The onion thrips (*Thrips tabaci* LINDEMAN, 1889) had already been considered a significant pest on horticultural crops even before it was first described by a Russian entomologist (DIAZ-MONTANO et al. 2011). This cryptic thrips species has received considerable attention ever since due to its importance as a polyphagous, cosmopolitan pest of several crop plants. Some aspects of its biology, ecology and management have been summarized in T. LEWIS's book, *Thrips as Crop Pests* (LEWIS 1997), followed by many other publications about other aspects of its ecology and management (DIAZ-MONTANO et al. 2011). Despite being one of the most intensively studied thrips species, several aspects of

* I would like to dedicate this paper to Irena ZAWIRSKA, whose early vision about the complexity of this species has been encouraging my research in this field.

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its biology remain unknown. The ultimate goal of this paper is to point out some of these unknown aspects.

TRHRIPS TABACI CRYPTIC SPECIES COMPLEX

T. tabaci had been known as a single cosmopolitan, polyphagous thrips species until ZAWIRSKA (1976) proposed that onion thrips had two distinctly different biological types. On the one hand, the “tabaci type” was found to reproduce by arrhenotoky, and its closely specialized strains fed on a small group of host plants, i.e. tobacco or deadnettle. On the other hand, the “communis type” had a different reproductive mode, namely, thelytoky and a broad range of host plants. She found a single morphological difference between the two types: the posteromarginal comb on the IXth abdominal tergites in larvae are present and absent in the “communis type” and “tabaci type”, respectively. She also observed a close interaction between the tobacco-feeding strains of the “tabaci type” and TSWV infections of tobacco. The possible host plants of the “tabaci type” were recently reviewed (JENSER et al. 2006) and 7 different plant species were reported as host plants only from Hungary. The “communis type” is widely regarded as a polyphagous pest (DIAZ-MONTANO et al. 2011). In an early study, several molecular genetic differences were found between three different onion thrips populations but the computed cluster analysis was unable to distinguish the populations (KRAUS et al. 1999). JENSER et al. (2001) reported characteristic molecular differences between populations of onion thrips collected from tobacco and onion. Despite all these reports, the proposition that onion thrips is not a single species but a complex of at least two (sub)species did not receive common acceptance until BRUNNER et al. (2004) published their paper on host-associated genetic differences in *T. tabaci*. Based on DNA sequences of the mitochondrial COI gene, *T. tabaci* has been divided into three lineages: a tobacco-associated type (T) and two leek-associated (L1, L2) ones. Later studies also confirmed three distinct groups within the *T. tabaci* cryptic species complex (TODA & MURAI 2007, KOBAYASHI & HASEGAWA 2012). It was proposed that the L1 lineage is arrhenotokous and the L2 lineage thelytokous (TODA & MURAI 2007). Based on the original description of onion thrips (LINDEMAN 1889) and the first report of different types within onion thrips (ZAWIRSKA 1976), the T lineage must be arrhenotokous. Although arrhenotokous and thelytokous female adults cannot be morphologically distinguished from each other, the use of recently developed primers has made the identification of the known L1 and L2 haplotypes of the onion thrips species complex more straightforward (TAKEUCHI & TODA 2011, KOBAYASHI & HASEGAWA 2012).

SPECIATION IN *TRHRIPS TABACI*

T. tabaci is believed to have originated in the eastern Mediterranean, from where its preferred host plant, *Allium cepa* LINNAEUS, 1753, is derived (MOUND 1997). According to this theory the L1 lineage of onion thrips is the form that most resembles the ancient type. It has been suggested that the T form of *T. tabaci* diverged from the ancient form around 28 million years ago (BRUNNER et al. 2004) and adapted to some native solanaceous host plants (for instance, *Solanum nigrum* LINNAEUS, 1753), and when tobacco was introduced to *T. tabaci*'s original distribution area a few hundred years ago, this form infested this new host plant (JENSER 2007). Both the L1 and T forms of *T. tabaci* reproduce by arrhenotoky, so mating between the two forms should be possible but has not yet been confirmed. It has been reported that *T. tabaci* populations collected from leek and tobacco plants both thrive on leek, but that those originally collected from leek failed to survive on tobacco (CHATZIVASSILIOU et al. 2002). This suggests that strong host fidelity is limiting gene exchange between the two forms, although it cannot be ruled out completely.

Around 21 million years ago yet another lineage, the L2 form, diverged from the ancient arrhenotokous form of *T. tabaci* (BRUNNER et al. 2004). The L2 form seems to be at a disadvantage when competing with the L1 lineage on onion. However, the L2 lineage seems to be better adapted to cabbage than the L1 form (LI et al. 2014). Nonetheless, both lineages perform reasonably well on both host plants, so it cannot be host fidelity that has been driving the divergence of L1 and L2 races. It has been reported that although arrhenotokous males attempted to copulate with thelytokous females, the males were rejected, suggesting the existence of reproductive isolation (TODA & MURAI 2007). The same behaviour between thelytokous females and arrhenotokous males was reported in the *Thrips nigropilosus* UZEL, 1895 species complex (NAKAO & YABU 1998). Reproductive isolation seems to be a logical key factor in the divergence of the L1 and L2 forms; this reproductive isolation requires detailed investigation, however. The first thelytokous individuals of *T. tabaci* might have been outcompeted on onion by the ancient L1 form, driving the specialization of L2 and adaptation to other host plants, like cabbage or other *Brassica* plants native in the eastern Mediterranean.

CONSEQUENCES

Identification of thrips species relies predominantly on external morphological features of slide-mounted adults. The use of dichotomous identification keys often presents a significant challenge to inexperienced scholars. More user-friendly interactive identification keys have become available recently, but they cover only a small fraction of

the described thrips species (MORITZ et al. 2001, 2004, 2009, 2013). The identification of larval thrips is even more difficult given the general lack of keys, so the recently published key for the larvae of Thripidae occurring in the Western Palaearctic is a major contribution in this field. Nonetheless, more keys are urgently required (VIERBERGEN et al. 2010). Theoretically, molecular identification keys could overcome the difficulties in identifying larval or other juvenile stages of Thysanoptera, but this tool is available only for a few dozen species (MORITZ personal communication).

DISTRIBUTION AND HOST RANGE

The distribution of *T. tabaci* lineages cannot be established with certainty according to the current state of knowledge. There is no known morphological difference between the adults of the three lineages of *T. tabaci*. Since the molecular genetic tools that enable the forms to be distinguished have been available for 10-15 years and much of the literature regarding the geographical distribution of *T. tabaci* was generated before this period, it is not always clear which form of *T. tabaci* was being reported. Even though there is no report about the successful application of artificial neural networks for distinguishing the entities of the *T. tabaci* cryptic species complex, this technique could have potential as it has been used to discriminate morphologically very similar species, namely *Thrips sambuci* HEEGER, 1854 and *Thrips fuscipennis* HALIDAY, 1836 (FEDOR et al. 2008, 2009, 2014). ZAWIRSKA (1976) reported a morphological difference between the larvae of the “tobacco type” and the “communis type”, corresponding to the T and L2 forms, respectively. However, larvae of the L1 and L2 forms cannot be distinguished in this way (unpublished, personal observation). Apart from all these difficulties, some published host associations may well be incorrect owing to invalid inferences having been drawn from the presence of adult thrips only on host plants, as MOUND (2013) has pointed out. Establishing the distribution and host plant range of the 3 known forms of *T. tabaci* by using only those reports in which the form is unambiguously identifiable would not yield the complete picture. Just to point out one example: based on the presence of *T. tabaci* males it is often concluded that the collected sample is arrhenotokous *T. tabaci*. However, it often cannot be determined whether males of the L1 or the T form have been encountered, since they might have some host plant species in common, on which both forms could complete their development, as has been reported for leek (CHATZIVASSILIOU et al. 2002). What is more, the presence of males does not prove that a given sample consists only of arrhenotokous specimens; the presence of thelytokous females among the arrhenotokous individuals would go undetected as they cannot be distinguished morphologically. Sympatric populations of at least two forms of *T. tabaci* have been reported (BRUNNER et al. 2004, NAULT et al. 2006,

KOBAYASHI et al. 2013, LI et al. 2014). Considering all the above-mentioned difficulties and limitations, there is only a limited number of reports that could be used to establish the true host range of the different *T. tabaci* forms. To do this, however, would go beyond the scope of this paper. To establish the distribution range of the 3 known forms of *T. tabaci* the currently available 249 accessions of the cytochrome oxidase subunit I (COI) gene in the GeneBank could be used, but this might not yield a complete result either. Even before this analysis is complete, it seems reasonable to assume that the thelytokous leek-associated (L2) form is polyphagous, the arrhenotokous leek-associated (L1) form has a relatively wide range of host plants as well, and the arrhenotokous tobacco-associated (T) form has the narrowest host plant range in this cryptic species complex. If the host range of the forms is confirmed to be similar to what is proposed here, it would indicate a great degree of host adaptation in the T form and smaller degrees in the L1 and L2 lineages. But this does not mean that there could be no performance differences between the L1 and L2 forms on different host plants, as one such report has already been published (LI et al. 2014). In that study, the L2 form of *T. tabaci* outcompeted the L1 type on cabbage plants. If this outcome turns out to be consistent between other populations of L1 and L2, it might be more accurate to identify L2 as the thelytokous cabbage-associated type.

ECOLOGICAL TRAITS OF THE *T. TABACI* FORMS

The divergence of the three known forms of *T. tabaci* have most likely led to the development of different ecological traits. The most obvious one is the appearance of thelytoky in the L2 form. Although endosymbiotic microorganisms are well-known for modifying the sex ratio in the progeny of arthropods, and thus induce thelytokous reproduction in otherwise arrhenotokous species, thelytoky in *T. tabaci* seems to be genetically inherited and not microbe-induced (NAULT et al. 2006, KUMM & MORITZ 2008). The lack of reports about a microbe-induced thelytokous *T. tabaci* population does not necessarily mean that none exists or used to exist in the ancient form of L2.

Adaptation to different primary host plants might also have led to divergence in the cues used in host recognition. The L2 form of *T. tabaci* did not respond to volatiles of 17 onion cultivars in a Y-tube olfactometer bioassay (DIAZ-MONTANO et al. 2012), but individuals of the same population showed a positive response to odours of 3 of the 6 tested white cabbage cultivars (FAIL et al. 2009). The adaptation of the L2 form to cabbage (or plant species of the *Brassica* LINNAEUS, 1753 genus) could explain the response of this form to some cabbage volatile organic compounds (VOCs). However, these VOCs have not been identified and the response of the L1 form to these compounds remains unknown.

The two types of leek-associated *T. tabaci* were found to coexist outdoors and the frequency of these two forms varied temporally (JENSER et al. 2006, NAULT et al. 2006), but the regulation mechanism remains unknown. Some thrips species undergo a reproductive diapause induced by short photoperiod: *Anaphothrips obscurus* (MÜLLER, 1776) (KAMM 1972); *Frankliniella intonsa* (TRYBOM, 1895) (MURAI 1987); *Limoithrips cerealium* HALIDAY, 1836 (LEWIS 1973); *Microcephalothrips abdominalis* (CRAWFORD DL, 1910) (NAKAO 1999); *Thrips nigropilosus* UZEL, 1895 (NAKAO 1993, 1994); *Thrips setosus* MOULTON, 1928 (NAKAO 1998, MURAI 2001). The critical day-length for diapause induction increases with latitude (MURAI 1987, NAKAO 2011). *Frankliniella occidentalis* (PERGANDE, 1895) seems to undergo no reproductive diapause under a short photoperiod (ISHIDA et al. 2003) and there is no published study about the response of the *T. tabaci* cryptic species complex to a short photoperiod. If there are differences between the forms in their response to a short photoperiod, this could be the mechanism regulating their temporal distribution.

TOSPOVIRUS VECTOR EFFICIENCY

One ecological trait of *T. tabaci* that has received considerable attention and has been studied extensively is its *Tospovirus* vector efficiency. Besides causing direct damage to its host plants, onion thrips is one of the 14 known thrips vectors of tospoviruses (RILEY et al. 2011). 20 *Tospovirus* species have been identified globally with 14 thrips species in the family Thripidae that can serve as vectors (ULLMAN et al. 1997, JONES 2005, PAPPU et al. 2009, CIUFFO et al. 2010, HASSANI-MEHRABAN et al. 2010). Thrips-transmitted tospoviruses (genus *Tospovirus*, family Bunyaviridae) are a major group of plant viruses with a wide host range. A single *Tospovirus*, the Tomato spotted wilt virus (TSWV), has at least 1090 host-plant species in 15 monocotyledonous and 69 dicotyledonous families worldwide (PARRELLA et al. 2003). PRINS & GOLDBACH (1998) estimated an annual loss of over \$1 billion worldwide from TSWV. Onion thrips vectors 3 tospoviruses (RILEY et al. 2011), two of which, TSWV and IYSV, occur in the European Union; the former has been established far longer. The management of TSWV epidemics in tobacco has recently been reviewed (JENSER et al. 2012). The different forms of *T. tabaci* differ in their ability to transmit tospoviruses. The arrhenotokous tobacco-associated lineage was reported to be highly effective in transmitting TSWV (CHATZIVASSILIOU et al. 2002), whereas the arrhenotokous leek-associated form transmits TSWV inefficiently (WIJKAMP et al. 1995, CHATZIVASSILIOU et al. 1999, 2002). By contrast, thelytokous populations did not transmit TSWV (WIJKAMP et al. 1995, CHATZIVASSILIOU et al. 2002) or transmitted it poorly (TEDESCHI et al. 2001), although recent studies have reported that some thelytokous

specimens are fairly efficient vectors (JACOBSON & KENNEDY 2013, WESTMORE et al. 2013).

It is reasonable to assume that the form of *T. tabaci* that is the most closely associated with TSWV by being adapted to the most common host plants of TSWV is the most efficient vector of this virus. This form is most likely the T form of *T. tabaci*. The characteristics that make this form an efficient vector could be inherited in various degrees by the progeny produced from interbreeding between the T and L1 forms. On the one hand, if a male of the T form mates with a female of the L1 form on leek, for instance, where they have been reported to form sympatric populations (CHATZIVASSILIOU et al. 2002), the female portion of the progeny could inherit TSWV vector efficiency to various degrees and they would all be identified as the L2 form, based on their maternally inherited COI gene. On the other hand, if the male is from the L1 form and the female is from the T form in the interbreeding pairs, then the female portion of the progeny might lose some of its characteristics responsible for efficient TSWV transmission, and they would all be identified as the T form, based on their maternally inherited COI gene. This could partly explain the reports about various levels of TSWV transmission efficiency among arrhenotokous *T. tabaci* (L1 and T forms). Specific insect-virus interactions have also been reported to influence variation in the vector efficiency of *T. tabaci* (JACOBSON & KENNEDY 2013).

The L2 form of *T. tabaci* has also been reported to transmit TSWV with varying efficiency. It seems likely that this variation is due to the different degree of adaptation between a given L2 haplotype and a TSWV isolate. The possibility of successful mating between arrhenotokous males (T or L1) and thelytokous females (L2) cannot be completely ruled out. Mating between individuals of 2 different reproductive modes in the *T. tabaci* cryptic complex has already been confirmed in a laboratory study (LI et al. 2015), and the observations reported by SOGO et al. (2015) from field populations of *T. tabaci* provided evidence that mtDNA from the thelytokous lineage must have introgressed into the arrhenotokous population in field conditions, which is consistent with the laboratory confirmation of productive mating and gene transfer from arrhenotokous to thelytokous *T. tabaci*. Onion and probably many other *Allium* species could have sympatric populations of all three *T. tabaci* forms; hence, there is no spatial or temporal barrier preventing successful mating between these 2 entities of *T. tabaci*. If successful mating is possible between the arrhenotokous and thelytokous forms of *T. tabaci*, then the L2 form might not have developed TSWV vector efficiency on its own but could have acquired it through mating with efficient vectors.

CONCLUSIONS

An increasing body of literature indicates that there could be significant differences in some economically important characteristics between the 3 known forms in the *T. tabaci* cryptic species complex. Therefore it is important to identify which form one is dealing with when investigating an ecological trait of this intriguing insect species. In order to avoid drawing false conclusions, some of the existing literature needs to be re-examined with regards to the applicability of the published features to the different forms of *T. tabaci*.

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