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Biological and morphological aspects of the onion thrips (*Thrips tabaci* Lindeman, 1889) species complex

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1. INTRODUCTION

Onion thrips (*Thrips tabaci* Lindeman, 1889) is a cosmopolitan insect pest of economic importance, causing significant damage to dozens of cultivated plant species, including alliaceous, cabbage and tobacco crops (JENSER and SZENASI 2004, TRDAN et al. 2006, DIAZ-MONTANO et al. 2011, LI et al. 2014, LOREDO VARELA and FAIL 2022). The pest status of *T. tabaci* is attributed to its polyphagous nature, high reproductive rate, short generation time, transmission of plant viruses, ability to reproduce without mating and development of resistance to insecticides (MORSE and HODDLE 2006, DIAZ-MONTANO et al. 2011). Economic damage results from direct feeding on over 300 host plant species, causing more than US $1 billion in crop losses worldwide each year (BALAN et al. 2018). *T. tabaci* has been identified as a vector of two economically significant viral pathogens, tomato spotted wilt virus (TSWV) and Iris yellow spot virus (IYSV), both of which cause additional plant damage. It is estimated that IYSW causes annual losses of U.S. $90 million to onion production in the western USA alone (GENT et al. 2006), whereas TSWV can cause over the U.S $1 billion in crop losses annually worldwide (GOLDBACH and PETERS 1994).

T. tabaci has received considerable attention due to its cryptic life habit and mode of reproduction. The existence of a cryptic species complex within *T. tabaci* was first reported by ZAWIRSKA (1976). The author proposed two biotypes within the species, the “communis type” and the “tabaci type” after finding considerable biological and ecological differences among onion thrips populations in Poland (ZAWIRSKA 1976). Since this first report, more information has been published, mainly referring to variation in reproductive mode, host plant preference, ability to transmit plant orthotospoviruses, and insecticide resistance among *T. tabaci* populations (ZAWIRSKA 1976, CHATZIVASSILIOU et al. 2002, WU et al. 2014). DNA sequences of the mitochondrial COI gene have confirmed that *T. tabaci* is a species complex, and it has been divided into three lineages: L1, L2 (leek-associated), and T (tobacco-associated) (BRUNNER et al. 2004). L1 leek-associated and T tobacco-associated lineages have arrhenotokous reproduction (TODA and MURAI 2007, FARKAS et al. 2020), while the L2 leek-associated lineage has thelytokous reproduction (KOBAYASHI and HASEGAWA 2012). Nevertheless, adults of the three lineages are considered indistinguishable based on their morphological features (JENSER et al. 2001, JENSER and SZENASI 2004, KOBAYASHI and HASEGAWA 2012). Size differences have been observed in some populations colonizing tobacco and onion plants in Iran (FEKRAT et al. 2014), but a detailed morphometric analysis of the three identified lineages has not been carried out so far.

T. tabaci has been one of the most intensively studied thrips species, though some of the biological aspects of this species remain unknown (FAIL 2016). Two lineages of *T. tabaci* exhibit a haplodiploid sex-determination system that allows parents to control their offspring's sex by different fertilization mechanisms. In two other haplodiploid species, the two spotted spider mite (*Tetranychus urticae* Koch) (MACKE et al. 2011b) and Kelly's citrus thrips, *Pezothrips kellyanus* (Bagnall) (KATLAV et al. 2020), sex allocation is mediated by egg size. In these two species, egg size determines not only larval size, juvenile survival, and adult size but also the probability of fertilization, with female (fertilized) eggs being larger than male (unfertilized) eggs. Since there are no further reports available for other haplodiploid arthropods, we intended to study this mechanism in the two arrhenotokous lineages of onion thrips.

Based on the studied literature on *T. tabaci*, which is well-known in several aspects, knowledge about the species complex is incomplete. To make a reliable decision and reduce the application of insecticides for the management of thrips, it is necessary to fully understand their biology, ecology, and population structure and to distinguish their biotypes. This Ph.D. project combines research on biological and morphological aspects of the *T. tabaci* species complex to better understand the mechanism of sex allocation in two arrhenotokous lineages of *T. tabaci*. Moreover, with a detailed morphometric analysis of the eggs, first instar larvae and adults, we intend to contribute to discrimination between lineages of *T. tabaci*.

1.1. Objectives

The main purposes of this Ph.D. project were to:

-Investigate the role of egg size on sex allocation in the two arrhenotokous lineages of the *T. tabaci* cryptic species complex by comparing the size of male and female eggs produced by mated mothers. Moreover, to determine if mating affects female resource allocation strategies, the eggs produced by virgin and mated females were compared, and finally, the consequences of sex allocation differences in male eggs produced by virgin and mated mothers were also investigated.

- Study the effect of maternal age on male and female egg size of virgin and mated mothers of the L1, L2 and T lineages of *T. tabaci*.

- Examine morphometric variability in the size of eggs, first instar larvae and adults of the *T. tabaci* cryptic species complex, to identify characters that may be useful in distinguishing between L1, L2, and T lineages.

- Study the development of sexual size dimorphism in the ontogeny of both L1 and T lineages of *T. tabaci* to identify if sexual size dimorphism is present in eggs, first instar larvae, or develop by adult emergence.

2. LITERATURE REVIEW

2.1. Sex allocation

Sex allocation is the most intriguing and productive study of evolutionary biology. Several theoretical and empirical works provide a powerful framework for understanding sex allocation. Sex allocation theory describes how parents should divide their investment of resources between male and female progeny in response to environmental conditions, and there are large numbers of supporting empirical studies (CHARNOV 1982, FLANAGAN et al. 1998, MARTINS et al. 1999, WEST et al. 2005, ABE et al. 2009). The theory of sex allocation states that under certain circumstances, the marginal fitness benefit of allocating resources to male or female reproduction differs, selecting for biased sex allocation (WEST et al. 1999, WILD and WEST 2009).

2.1.1. Fisher's principle for an equal sex allocation

In sexual reproduction, most species produce approximately an equal number of males and females (1:1).This biological phenomenon remained unsolved until FISHER(1930) proposed that this is a result ofthe natural selection mechanism. Although this argument advanced by Fisher was predated by DARWIN (1871) in the first edition of "The Descent of Man". This was turned into mathematical form and presented by DUSING in 1883 (EDWARDS 2000). Fisher was the first to explain why this proportion prevails, regardless of sex-determination mechanisms. According to Fisher's principles, when the effort required to produce each of the two sexes is equal, the population sex ratio remains constant at 1:1; if the effort is unequal, than one sex has an advantage. To determine fitness consequences when individuals bias their offspring's sex ratio, it requires a system in which equilibrium is expected to be achieved but in which deviations from Fisher's 1:1 ratio may occur under certain conditions. Fisher's theory of equal investment is the progenitor of all sex allocation theories.

2.1.2. Group structure leads to biased sex ratios

Fisher's 1930 argument assumption for equality, according to HAMILTON (1967), may fail where there is competition and cooperation among relatives, which may favour biased sex allocation. Interaction between relatives has been suggested as an explanation for biased sex allocation in a wide range of organisms, including mammals, birds, reptiles, insects and plants. These interactions can be divided into two broad categories: local resource competition (encompassing competition for

resources beyond mating opportunities but including competition between siblings and parent-offspring competition as well) and local resource enhancement.

2.1.2.1.Local resource competition

Sex allocation in response to local resource competition was suggested to explain the male-biased sex ratio as hypothesized by CLARK (1978). In mammalian species, sons disperse from natal groups while daughters remain near to birthplace, and whenresources are limited, they compete with the mothers for access to resources, while dispersed males compete with unrelated individuals in non-natal groups. CLARK (1978) proposed that under such conditions, female competition could be reduced if females uniformly biased the sex ratio of their offspring in favour of males, resulting in less competition.

2.1.2.2.Local resource enhancement

Local resource enhancement occurs when there is cooperative interaction between relatives. For example, if daughters are the most helpful sex inhelping their parents to defend their territories and rear their offspring,thus providing fitness to their parents by their own reproduction or directly enhancing the parent's reproductive success. In this case, the most unbeatable strategy is to invest in the sex that is more beneficial to the parents. As a result, the progeny sex is determined by the presence or absence of helpers. Most examples of local resource enhancement come from birds (TRIVERS and WILLARDS 1976, GOWATY and LENNARTZ 1985, KOMDEUR et al. 1997, WEST and SHELDON 2002), but it can occur outside of birds as well. In African wild dogs (*Lycaonpictus*), females disperse from the pack after weaning while males remain to help, and the observed sex ratio in the field is 0.6 (MALCOM and MARTEN 1982).

2.1.3. Local mate competition

A particular case of competition between relatives is the local mate competition developed by HAMILTON (1967). It predicts that when populations are structured and subdivided such that related males compete with each other for mates and mating occurs between siblings, there will be a female-biased sex ratio. The local mate competition model has been able to explain biased sex ratios in many organisms, such as wasps, fig wasps, mites, aphids, protozoan parasites, beetles, spiders, barnacles, and snakes (WERREN 1980 and 1983, CHARNOV 1982, HERRE 1985, MADSEN and SHINE 1992, WRENSCH and EBBERT 1993, SHUTLER and READ 1998, HARDY 2002, NEE et al. 2002, REECE et al, 2008). The theory of local mate competition states that female optimal offspring

depends on the level of local mate competition, ranging from highly female-biased under strong local mate competition to unbiased in Panmixia (HAMILTON 1967). Empirical approaches indirectly support this prediction by demonstrating that individuals can adjust their offspring sex ratio based on the intensity of local mate competition. Furthermore, in the spider mite *Tetranychus urticae*, experimental evolution under strong and constant local mate competition has been shown to inhibit phenotypic plasticity in sex allocation (MACKE et al. 2011a).

2.2. Sex allocation in response to the environment

One of the most influential theories in sex allocation is the Trivers-Willard hypothesis. It states that natural selection favours a parent's ability to adjust their offspring's sex ratio in a direction that maximizes their reproductive fitness (TRIVERS and WILLARD 1973). They proposed that when mothers are in good conditions, they preferentially produce sons, whereas when mothers are in poor conditions, they preferentially produce daughters, because sons in good conditions are expected to out-reproduce daughters in good conditions, and daughters in poor conditions are expected to out-reproduce sons in poor conditions. Specifically, the Trivers-Willard predictions rest on three assumptions. First, paternal conditions should be correlated with offspring conditions. Second, offspring conditions persist into adulthood, and third, differences in adult conditions affect the reproductive success of males and females.

2.3. Constrained sex allocation

The constrained model (GODFRAY 1990) is a specific model of the sex ratio in haplodiploid species. In haplodiploid animals, virgins or sperm-depleted females can still reproduce but are constrained to produce only male offspring. This excess of male production by a constrained female (virgin) can lead an unconstrained female (mated) in panmictic populations to adjust their sex ratio in favour of females and compensate for the excess of males in populations. According to the theory of constrained sex allocation, if a percentage of females remain unmated and produce only male offspring, the mated female will evolve to have a female-biased sex ratio (GODFRAY 1990). This phenomenon is mainly associated with virginity, but can also occur after mating due to insemination failure, selfish genetic elements, and physiological constraints. Such constraint sex allocation has been extensively studied in hymenopterans (ODE et al. 1997, WEST et al. 1999, METZEGER et al. 2008), but less in other taxa of haplodiploids (HIGGINS and MYERS 1992, KRANZ et al. 2000). Females of the parasitoid wasp *Uscana semifumipennis*, for example, produced more male-biased offspring when mated with smaller males, owing to their lower sperm quality or quantity

(HENTER2004). Another factor of constrained sex allocation is maternal fitness (TRIVERS and WILLARD 1973, CHARNOV 1982). Constrained sex allocation in *Pezothrips kellyanus* is determined by maternal body size; lower fitness-constrained mothers have a smaller body size, which limits egg provisioning due to the size scaling constraint of spermatheca and thus limits sperm access to the smaller eggs, as it has been demonstrated that egg size determines fertilization success (KATLAV et al. 2021).

2.4. The evolution of the haplodiploid sex determination system

Of particular interest to the sex allocation field is the haplodiploid sex-determination system, which has evolved in 15% of arthropods (DE LA FILIA 2015). The ability of haplodiploids to precisely control the sex ratio of their offspring is well documented (BULL 1983). Haplodiploidy is a sex-determination system in which males are produced from unfertilized eggs and females from fertilized eggs. Arrhenotoky is one form of haplodiploidy. Under arrhenotoky and another type of haplodiploidy, paternal genome elimination (PGE), gene expression in males is haploid and maternally inherited (single set of chromosomes), while females are diploid (two sets of each of the chromosomes). The consequence of this mode of reproduction is that males only pass their genes on to their daughters. As sons have no fathers on haplodiploid lines, their closest male progenitors are their maternal grandfathers. On the other hand, females gain fitness benefits through both sons and daughters. Haplodiploidy has evolved in the vast majority of Hymenoptera (bees, ants, wasps, and sawflies) and Thysanoptera (thrips), where all species are haplodiploid, but it can also occur in Hemiptera (whiteflies) and a few beetle species (VAN DER KOOI et al. 2017). Most theories assume that haplodiploidy has evolved from maternal-paternal genetic conflicts (HARTL and BROWN 1970, BULL 1979).

2.5. Sexual conflicts over sex ratio in haplodiploids

It is generally assumed that each parent contributes an equal share of their genes to their offspring. Decisions over what sex ratio to produce can have evolutionary consequences for both parents and offspring. However, the extent to which males and females come into evolutionary conflict over the sex allocation patterns depends on the genetic system, when genes are passed unequally to the next generation by the two sexes (SHUKER et al. 2009). In such cases, sexual conflicts are thought to promote the evolution of sex chromosomes. In haplodiploids, female genes are passed on to both males and females, whereas males can pass their genes only to daughters. This implies that natural selection would favour male adaptations that induce the production of daughters

by the females with whom they were produced. For example, males may transfer seminal fluid proteins that affect the fertilization rate by increasing the sperm release from the spermatheca (SHUKER et al. 2009). This effort of males to influence daughter production leads to sexual conflict between males and females over the sex ratio of the progeny. MACKE et al. (2014) showed that the levels of local mate competition modulate sexual conflicts over sex ratio in haplodiploids, leading to the evolution of manipulative traits and fathers' can affect sex ratio, challenging conventional assumptions.

2.6. The influence of endosymbionts on sex allocation in haplodiploids

Maternally inherited bacterial endosymbionts are very widespread in many haplodiploid arthropod species. Several theoretical studies have shown that maternally inherited endosymbiosis may facilitate haplodiploidy evolution (NORMARK 2004, ENGELSTÄDTER and HURST 2006). There are several main intracellular bacterial genera that are known to infect arthropods, such as *Wolbachia*, *Rickettsia*, *Cardinium,* and *Spiroplasma*. These bacterial endosymbionts are vertically transmitted from the infected mother to their eggs and are known to alter reproduction in their arthropod host by a variety of mechanisms: (1) by causing cytoplasmic incompatibility; (2) by biasing the sex ratio in favour of females via either male killing or through the feminization of genetically male individuals; or (3) by inducing parthenogenesis (CHARLATet al.2003, ENGELSTÄDTER and HURST 2009). Only *Wolbachia* is shown to cause all these phenotypes, whereas for *Cardinium* there is evidence for all these phenotypes except male killing. In contrast, other bacteria are known to cause the male-killing phenotype, and *Rickettsia* can also induce parthenogenesis (GOODACRE and MARTIN 2012). In haplodiploid arthropods, at least three taxa are involved in endosymbiont-induced parthenogenesis: *Wolbachia*, *Cardinium,* and *Rickettsia* (STOUTHAMER et al. 1993, ZCHORI-FEIN et al. 2001, HAGIMORI et al. 2006). Although *Wolbachia*-induced cytoplasmic incompatibility and male-killing are likely the most common phenotypes, evidence for *Wolbachia*-induced parthenogenesis has been reported in three arthropod orders: Hymenoptera, Thysanoptera, and Acarina (STOUTHAMER et al. 1993, WEEKS and BREEUWER 2001). *Wolbachia* is estimated to be present in 40% of all arthropod species (ZUG and HAMERSTEIN 2012). *Wolbachia* has been found to induce parthenogenesis in *Hercinothrips femoralis* (O.M. Reuter) and *Heliothrips hemorrhoidalis* (Bouché) (PINTUREAU et al. 1999). In *Franklinothrips vespiformis* (Grawford) and *Taeniothrips inconsequens* (Uzel), thelytokoy is induced by *Wolbachia* infection; thus, in the absence of *Wolbachia*, both species are arrhenotokous. (MORITZ 1997, ARAKAKI et al. 2001). Cytological

examination of ovaries in *T. tabaci* populations using diagnostic polymerase chain reaction revealed no evidence of *Wolbachia* in either thelytokous or male-producing populations (NAULT et al. 2006, KUMM and MORITZ 2008). GAWANDE et al. (2019) reported for the first time the presence of *Wolbachia* in *T.tabaci*; it was detected at 0.56% of total Operational taxonomic units (OTUs), but its role in *T. tabaci* is unclear. Even though *Wolbachia* association is very common in arthropods (WERREN 1997), its prevalence within species may vary from very low to high (HILLGENBOECKET et al. 2008). KUM and MORITZ (2008) observed both infected and uninfected individuals in the thrips, *Sucerathrips linguis* (Mound & Marullo) and *Gynaikothrips ficorum* (Marchal). JACOB et al. (2014) reported that populations of *Scirtothrips cardamomi* Ramak collected from different agro-systems showed a variable level of infection, ranging from 15.0 to 87.8%.

Endosymbiont-induced parthenogenesis is easy to reveal in haplodiploid taxa. The main approach to revealing the bacteria-induced parthenogenesis is by curing the parthenogenetic females of their endosymbionts via antibiotics and/or heat treatments that remove endosymbionts and lead to the production of sons instead daughters. This approach provides direct evidence for the role of endosymbiont-induced parthenogenesis in their host (STOUTHAMER et al. 1993) and has been used to reveal endosymbiont-induced parthenogenesis in haplodiploid taxa such as mites, thrips, and wasps. In practice, if parthenogenesis has genetic causes and is not induced by endosymbionts, treated females should continue to produce female progeny.

2.7. Male influence in sex allocation in haplodiploids

It is generally assumed that females have substantial control over sex allocation, especially in haplodiploid species, females determine sex by deciding whether or not to fertilize each egg (resulting in a diploid female egg or a haploid male egg) (SHUKER et al. 2006). Male influence in sex allocation has been considered to have little effect because it is not clear how they can influence the sex ratio (WERREN and BEUKEBOOM 1998), although this is perhaps a result of a lack of studies. Mechanisms by which males influence sex allocation are not straightforward, and their potential influence on sex ratios is underestimated. Males may influence sex allocation in three different ways (HENTER 2004). First, the ability of males to fertilize eggs varies, with some males producing sperm that is unable to successfully fertilize eggs. Second, the incompatibility of the paternal and maternal genomes leads to the embryonic death of daughters. Third, the attempt of the male to increase daughter production is because males can only pass genes to their daughters (HAWKES 1992).

MACKE et al. (2014) reported that males can influence the relative proportion of males and females in the progeny of *Tetranychus urticae* under high levels of sexual conflicts. Other studies in parasitoid wasp *Nasonia vitripennis* (Walker) show that some of the variations in the sex ratio of the offspring can be attributed to the males when comparing the effect of male strain on the sex ratio (SHUKER et al. 2006), suggesting that males can also influence the female sex ratio and contribute to the variations around the sex ratios optimal for females. However, the influence is not so large, suggesting that females have more influence in sex allocation than males.

2.8. The influence of egg size on sex allocation

Sex allocation is the most important reproductive aspect of animal reproduction and involves parental control over the production of male and female offspring (CHARNOV 1982, WEST 2009). Parents may achieve this by varying the number of sons versus daughters (i.e., biased sex ratio: (HARDY 2000), and this was widely studied in various animals with different sex determination mechanisms (HAMILTON 1967, KOMDEUR and PEN 2002). However, increasing the relative number of the preferred sex is not the only way by which parents can adjust sex allocation. Sex allocation can also involve differential investment into male versus female offspring (PETRIE et al. 2001, MAGRATH et al. 2004). And this may be done to alter the quality of these eggs by providing them with different amounts of resources (FOX and CZESAK 2000). Such parental investment in eggs can thus dramatically influence offspring fitness, and one of the most widely used predictors of such investment is egg size. However, few studies have investigated the adjustment of egg size depending on the sex of the embryo. Such sex-biased paternal strategies have been proven in birds (ANDERSON et al. 1997, CORDERO et al. 2001, BADYAEV et al. 2006, SAINO et al. 2010) and in lizards (RADDER et al. 2009). In two haplodiploid arthropods, egg size- mediated sex allocation has been reported for the two-spotted spider mite *Tetranychus urticae* Koch (MACKE et al. 2011b) and Kelly's citrus thrips *Pezothrips kellyanus* (Bagnall) (KATLAV et al. 2021). In these two species, egg size determines not only larval size, juvenile survival, and adult size but also the probability of fertilization, with female (fertilized) eggs being larger than male (unfertilized) eggs. Yet, the mechanisms of egg size-dependent fertilization remain unknown.

2.9. Factors influencing egg size

2.9.1. The trade-off between egg size and number

The size and number of offspring produced by organisms are key parameters in their life histories as they are major components of fitness. The life history theory predicts that there should be an inverse relationship between offspring size and number because resources are limited and females cannot simultaneously maximize both (STEARNS 1992). SMITH and FRETWELL (1974) predict a negative relationship between egg size and number, suggesting that a particular combination must exist for each species to maximize fitness. The offspring size vs. number trade-off relies on the assumption that larger offspring tend to have higher adult reproductive success and a better chance for survival into adulthood. If resources are unlimited, a female should invest more resources per offspring to enhance her reproductive success. On the other hand, if resources are limited, a female should increase the size of her offspring at a cost to the number of offspring produced, and this is supported by numerous studies in insect species (CARRIERE and ROFF 1995, FOX et al. 1997, SAVALLI and FOX 2002, FISCHER et al. 2003a, FISCHER et al. 2003b, ROTEM et al. 2003, TAKAKURA 2004).

2.9.2. Maternal age effect on egg size

Maternal age influences the egg size of many species of insects. In mostinsect species, egg size decreases with increasing maternal age (FOX 1993), while in some other studies, egg size increases with increasing maternal age (KASULE 1991); egg size being independent of maternal age has also been reported (BERGER 1989, MARSHALL 1990). The decrease in egg size with increasing maternal age is often attributed to the female nutritional status and nuptial gifts that females receive during mating. FOX (1993) compared the eggs laid by females with and without food in *Callosobruchus maculatus*. Older females laid larger eggs when they had food and water than when they did not. The decrease in the egg size when females are in stressful conditions results from the depletion of female resources. YANAGI and MIYATAKE (2002) reported similar results in a related species, *Callosobruchus chinensis*. In many insect species, males donate nutrient benefits to females during their ejaculation, and females use these nutrients for egg production and somatic maintenance. Male-derived substances have been detected in oocytes and female somatic tissues of many insect species (BOGGS 1990). In some of the species, the benefit of this transfer of nutrition during copulation has not been detectable (JONES et al. 1986, SVARD and WINKLUND 1988, WEDELL and ARAK 1989); while in some others, the benefits to the females have been detected only when females were under nutrient stress (GWYNNE 1984, GWYNNE et al. 1984, BOUCHER and HUIGNARD 1987). Also consistent with the resource depletion hypothesis is the fact that *C.*

maculatus females laid larger eggs when they mated multiple times than when they mated once (FOX 1993). Multiple mating has been observed to increase egg size in crickets and katydids (GWYNNNE 1984, SIMONS 1988). If a change in the egg size is mediated by a female's nutritional status, then the behaviours that influence the nutritional status will influence egg size and possibly offspring life histories indirectly.

2.10. Onion thrips classification and diagnosis

2.10.1. Classification and identification

Thrips are soft-bodied, slender insects with fringed wings in the order Thysanoptera, which has nearly 7700 species and over 1200 genera (Table 1) (MOUND 2022), in which two suborders are recognized, Terebrantia and Tubulifera (MOUND et al. 1980). The former comprises species from eight families, with the largest family being the Thripidae. Thrips of the suborder Tubulifera are represented by only one family, Phlaeothripidae, which is the largest family of Thysanoptera (MOUND 1997).

Table 1. Classification of *Thrips tabaci*

Order	**Suborder**	**Family**	**Sub-family**	**Tribe**	**Genera**
Thysanoptera	Terebrantia	Thripidae	Thripinae	Thripini	*Thrips*

T. tabaci was first described by a Russian entomologist, Karl Eduard Lindeman, based on specimens that caused damage to tobacco plants (LINDEMAN 1889). It is believed that it originated in the eastern Mediterranean, from where its preferred host plant, *Allium cepa* Linnaeus, is derived (MOUND 1997). Because of its adaptability to a wide range of environmental conditions, it is now found all over the world, and its small size makes it difficult to detect by phytosanitary inspections. Like in any insect group, the identification of thrips species includes a wide range of alternatives and specific methods (MEHLE and TRDAN 2012), from printed dichotomous keys to more user-friendly pictorials (MOUND and KIBBY 1988) and complex multi-access keys (MORITZ et al. 2001). Genetic markers are a powerful tool in the identification of thrips species, including their immature stages (MORITZ et al. 2000, BRUNNER et al. 2002). An interactive electronic system created by MORITZ et al.(2004b) combines both morphological and molecular information. Several other studies (FEDOR et al. 2008, 2009, KUCHARCZYK and KUCHARCZYK 2009, KUCHARCZYK et al. 2012) underline morphometric (both quantitative and qualitative) variables as an autonomous

tool for thrips identification, in the sense of either basic multivariable analyses (e.g., principal component analyses) or even the phenomenon of more complex artificial neural networks (ANNs).

2.10.2. Diagnostic characters of *Thrips tabaci*

The accurate identification of *T. tabaci* is crucial for any study, particularly in formulating effective pest management strategies. Despite several modern techniques for identifying thrips species, a morphological identification key is usually an indispensable first step in thrips species identification. Different species of thrips are generally similar in appearance, differing only in minute details, so accurate determinations of thrips species require the use of diagnostic keys. Conventional insect taxonomy mostly relies on external morphology-based dichotomous keys for species delimitation. Several identification keys are available for the identification of thrips specimens (MOUND and WALKER 1982, MORITZ 1994, MOUND and KIBBY 1998, MOUND and MASUMOTO 2005, ZHANG et al. 2011, MOUND et al. 2016, CLUEVER and SMITH 2017, BELAAM-KORT 2020). The main diagnostic characteristics that distinguish adult *T. tabaci* from other thrips species are listed in Table 2.

Table 2. Characters of adult *T. tabaci*

Antennae	**7 segmented**
	I pale, II-VII yellowish brown, III-V with pale bases
	Segments III-IV with forked sense cones
	VII short
Ocellar setae	Only two pairs
Pronotum	Two pairs of posteroangular setae
	Posterior margin with 3 or 4 pairs of setae
Mesonotum	Without anterior pair of campaniform sensilla
Metanotum	Irregularly reticulate medially with lines covering to midpoint near the posterior margin
	Median setae short and arising behind anterior margin
	Campaniformsensilla absent
Forewings	Posterior fringe cilia on forewings wavy
	4 (2-6)distal setae on the forewing first vein
Abdominal tergites	Tergite II with 3 lateral marginal setae

	Tergite VIII with a complete comb
	Ctenidia present on abdominal segment V-VIII, on VIII posteromesad to spiracles
	pleurotergites without discal setae but with the sculpture of rows of fine microtrichia
Abdominal sternites	Lack of accessory setae
	Sternite II with 2 pairs of marginal setae
	Sternite III-VII with 3 pairs of marginal setae
	The median pair on VII arising in front of the margin

T. tabaci can be easily distinguished from other thrips species by the closely spaced rows of microtrichia on the pleurotergites (MORITZ et al. 2004b, MOUND and MASUMOTO 2005).

2.11. Life cycle and reproduction of *Thrips tabaci*

2.11.1. Life cycle of *Thrips tabaci*

The life cycle of *T. tabaci* consists of an egg, first and second instar larvae, pre-pupae, pupae, and an adult (GHBAN 1974, NAKAHARA 1991). Despite being classified as Hemimetabola, Thysanoptera does not have typical hemimetabolous stages. At first sight, comparisons of larvae with adults show many similarities, which suggest that there is little need for a major transformation of larvae into an adult. However, investigations of the anatomy during the quiescent prepupa and pupa show that many imaginifugal characters are broken down and reformed during the transition from second instar larvae into adults (MORITZ 1995). The development of thrips is an intermediate between hemi and holometabola. The egg, two larval instars, and adult can be found in the host, while the two pupal instars are inactive and can be found in the soil or among leaf litter (POURIAN et al. 2009). As with all Terebrantia, the eggs of *T. tabaci* are inserted singly into leaf tissue. They are microscopic, whitish at oviposition, and kidney-shaped. As eggs mature, they change to an orange tint with two red spots representing the larval eyes. Only one edge of the egg is close enough to the tissue surface to allow the immature to emerge. On onion, the average length of the egg is 0.23 mm and the average width is 0.08 mm (PATEL et al. 2013). There are two active feeding stages. The first-instar larvae are semitransparent and white, changing later to yellowish-white. It is small (0.35-0.38 mm in length) and starts feeding very quickly. The second-instar larvae are larger and yellow (PATEL et al. 2013). Larvae are 0.7-0.9 mm in length with red eyes. In general, larvae of the family Thripidae have seven segmented antennae, a pair of spiracles on the mesothorax, and a pair of spiracles in

segments II and VIII of the abdomen. In the case of *T. tabaci,* these spiracles are present only in the first instar larvae, whereas in the second instar larvae, the spiracles are present only in the mesothorax and segment VIII of the abdomen. First and second instar larvae differ by the number of setae on the pronotum and abdominal segments III-VII; first-instar larvae have 6 pairs of setae on the pronotum, while second-instar larvae have 7. The first instar larvae have 2 pairs of sternal setae on abdominal segments II-VII, and the second instar larvae have 3 pairs. (VIERBERGEN et al. 2010). Prepupa and pupa are relatively inactive and non-feeding stages. Pupation normally takes place at the base of the plant's apical meristem or within the soil (RUEDA and SHELTON 1995). The average length and width of prepupae are 0.9 mm and 0.23 mm, respectively. The prepupae are whitish to yellow and the duration of prepupae is 1-3 days. The pupae are yellowish-white changing to yellow before adult emergence. The prepupae and pupae differ from the larvae because of the presence of wing sheaths (GHABN 1948). The prepupa and pupa can be recognized by their developing wing pads and the orientation of the antennae (GHABN 1948). In the pupa stage, the antennae are folded back over the head, and the wing pads become well-developed (PATEL et al. 2013). Adults are more mobile than the two immature instars and pupal stages. Adults usually fly and land on exposed clothes or skin due to the attraction of the white and yellow colours. The body colour varies with temperature, from yellow to dark brown (MURAI and TODA 2002), and is usually palest when developing under high temperatures (MOUND and WALKER 1982). Female adults are 1.0-1.3 mm in length (MORISON 1957), and male adults are 0.7 mm in length (PERGANDE 1895).

2.11.2. Reproductive modes of *Thrips tabaci*

T. tabaci can reproduce asexually through parthenogenesis and sexually (GILL et al. 2015). Three reproductive modes have been reported in *T. tabaci* populations: thelytoky, arrhenotoky (LEWIS 1973, JENSER and SZÉNÁSI 2004), and deuterotoky (NAULT et al. 2006). The most common reproductive mode is thelytoky (LEWIS 1973, KENDALL and CAPINERA 1990), in which females are produced parthenogenetically from unfertilized eggs. *T. tabaci* is known to reproduce also by arrhenotoky (KENDALL and CAPINERA 1990), a type of parthenogenesis in which females are produced from fertilized eggs and males from unfertilized eggs. Deuterotoky is an uncommon mode of reproduction that occurs when unfertilized eggs develop into either males or females (SUOMALAINEN and SAURA 1993). The two reproductive modes, arrhenotoky, and thelytoky, are genetically different (TODA and MURAI 2007, KOBAYASHI and HASEGAWA 2012) and co-occur in the field (LI et al. 2014). While deuterotoky was reported twice, one in L1 and L2 lineages

of *T. tabaci* collected from onion fields in the USA (NAULT et al. 2006) and another time in Hungary from specimens originally phenotyped as arrhenotokous (WOLDEMELAK 2020). Deutorotoky within the order Thysanoptera has been only reported in onion thrips and *Apterothrips apteris* (Daniel) (Mound 1992).

The majority of published studies relate thelytoky to L2 lineage and arrhenotoky to L1 and T lineages of onion thrips. Besides the different reproductive modes and adaptations to their lifestyle, there is evidence indicating that the reproductive modes of the *T. tabaci* cryptic species complex might not be a fixed phenotype (SOGO et al. 2015, AIZAWA et al. 2016, JACOBSON et al. 2016). SOGO et al. (2015) found that both arrhenotokous and thelytokous *T. tabaci* populations coexisted in *A. tuberosum* and *A. fistolousum* crops in Japan; most of the virgin females phenotyped as arrhenotokous and thelytokous were grouped within the L1 and L2 clades, respectively. Only two arrhenotokous virgin females were grouped within the L2 lineage (generally associated with thelytoky) based on differences in the maternally inherited mtCOI genetic marker. AIZAWA et al. (2016) reported similar findings, as only a few individuals phenotyped as arrhenotokous had mtCOI sequences that placed them within the L2 lineage. Based on these studies, caution is needed when concluding about the reproductive mode based on genetic markers alone. The various reproductive systems of *T. tabaci* contribute to its becoming more problematic because, for example, thelytokous individuals do not depend on finding mates, and if they are resistant to any insecticide, their offspring will be too (DIAZ-MONTANO et al. 2011).

2.12. The known differences between lineages of *T. tabaci*

There are biological and ecological differences between the different lineages of *T. tabaci*. The L1 lineage of *T. tabaci* performed better on onions than in cabbages, whereas in the L2 lineage the opposite occurred (LI et al. 2014). The significant difference between T and L2 of *T. tabaci* has been reported regarding TSWV vector transmission efficiency. Transmission studies have shown variation in the competence of *T. tabaci* as a vector of TSWV (JACOBSON et al. 2013, WESTMORE et al. 2013). Both poor and efficient transmitting populations have been observed in Europe, Australia, and the United States (WILSON 2001, CHATZIVASSILIOU et al. 2002, JENSER et al. 2004, JACOBSON and KENNEDY 2013, WESTMORE et al. 2013). Arrhenotokous populations collected from tobacco (currently recognized as T lineage) were highly effective in transmitting Tomato spotted wilt virus (TSWV) (CHATZIVASSILIOU et al. 2002), whereas arrhenotokous populations collected from leek (currently recognized as L1 lineage) transmitted efficiently TSWV (CHATZIVASSILIOU

et al. 2002). In contrast, the thelytokous population (currently recognized as L2 Lineage) did not transmit TSWV (WIJKAMP et al. 1995, CHATZIVASSILIOU et al. 2002), or transmitted it poorly (TEDESCHI et al. 2001). Although some recent studies reported that the L2 lineage could also transmit TSWV (JACOBSON and KENNEDY 2013, WESTMORE et al. 2013). *T. tabaci* is a widely distributed insect pest of economic importance (FAIL 2016). Its presence is reported in over 120 countries and territories (CAB INTERNATIONAL 2021). It ranges from tropical to subtropical and also occurs in temperate regions (POURIAN et al. 2009). *T. tabaci* is a major pest of fields and greenhouse plants all over the world. It is hosted not only in the leaves but also in the flower of its host plant when it feeds on pollen (MURAI 2000), and because of its small size, it can easily be airborne and transmitted by the wind and other transportation means. Because of the wide variety of host plants, wide geographical distribution, and reduced susceptibility of *T. tabaci* to insecticides, it appears likely that different *T. tabaci* lineages exist in different host plants and locations around the world. The host plant association and the geographical distribution of the onion thrips at the lineage level have been recently reviewed by LOREDO VARELA and FAIL (2022). Based on this study, the leek-associated L2 is the only lineage with a confirmed worldwide distribution and has the broadest host range, including major crops from different plant families. The distribution of the L1 leek-associated lineages is limited to a few dozen countries and it shares some host plants with the L2 leek-associated lineage but is often found in Allium crops. While the T tobacco-associated lineage has only been found in tobacco plants and associated weeds in central and Eastern Europe and the Middle East. Regardless of the lineages, 391 plant species were reported as host plants in which the breeding and development of *T. tabaci* occurred. These host plant species come from 64 different families, with the most important ones being Asteraceae, Fabaceae, Brassicaceae, Poaceae, and Solanaceae. (LOREDO VARELA and FAIL 2022). Knowing the breeding sites of onion thrips has a direct impact on successful pest management strategies.

Moreover, the lineages of *T. tabaci* has shown various susceptibility to the insecticides. TODA and MORISHITA (2009) were the first to discover three nonsynonymous nucleotide substitutions in the para-orthologous sodium channel gene of the L2 lineage of *T. tabaci*. They create amino acid substitutions M198T, T929I, and L1014F, which are responsible for pyrethroid-resistance in the L2 lineage of *T. tabaci* but also in other insect species (DAVIES et al. 2007). WU et al. (2014) discovered new mutations in the sodium channel of *T. tabaci*, resulting in amino acid changes M918L and V1010A that are responsible for lambda-cyhalothrin resistance in populations derived from red onions. However, they did not provide information for more precise identification of the species

complex from their samples collected in the USA, so their results most likely refer to the L1 or L2 lineage. NAZEMI et al. (2015) showed that enhanced detoxification, implicated by the use of inhibitors of major metabolic enzymes (P450 monooxygenases), is responsible for resistance to organophosphates (profenofos and chlorpyrifos) in onion populations in Iran. He reported as well that in deltamethrin resistant populations, the aminoacid substitution T9291 was detected to confer pyrethroid resistance. ROSEN et al. (2021) found that resistance to spinosad is associated with metabolic enzymes (P450) by increasing the levels of detoxifying among resistant populations of *T. tabaci* in Izrael; however, resistant populations were more fecund compared to susceptible ones, suggesting a lack of fitness cost of the resistance trait. Although studies in western flower thrips have shown that the main mechanism associated with the resistance to spinosad is mainly due to target site mutations (SPARKS et al. 2012, PUINEAN et al. 2013). In Japan, pyrethroid resistance was investigated in connection with the reproductive modes of *T. tabaci*. It was reported that only the thelytokous population encoded M918T, L1014F, whereas both thelytokous and arrhenotokous populations encoded the T9291 (TAKEZAWA 2012, YOKOYAMA and KASHIMA 2013, AIZAWA et al. 2016, AIZAWA et al. 2018). In the study by AIZAWA et al. (2018) all *T. tabaci* strains with cypermethrin resistance had the T9291 mutation in the sodium channel. In that study, all 53 arrhenotokous strains were deemed cypermethrin-resistant, whereas only four thelytokous strains were deemed cypermethrin-resistant, out of 34 thelytokous strains. The authors also discussed the link between cypermethrin resistance and the biotic performance of arrhenotokous and thelytokous reproduction strains. The development, longevity, and fecundity of the resistant arrhenotokous strain were higher than those of the resistant thelytokous strain. The resistant arrhenotokous strain exhibited similar longevity and fecundity to the susceptible thelytokous strain. Their results suggested that cypermethrin resistance conferred by T9291 affects longevity and fecundity negatively in the thelytokous strains. Only a few limited studies show what kind of fitness cost occurred in resistant strains versus susceptible strains.

Furthermore, the use of molecular methods has advanced our understanding of some biological and ecological phenomena in the *T. tabaci* cryptic species complex, such as the gene flow from arrhenotokous lineage to thelytokous lineage (LI et al. 2015, JACOBSON et al. 2016), the occurrence of sympatric populations of two *T. tabaci* lineages (KOBAYASHI et al. 2013) the reproductive isolation of the so called leek associated lineages from the tobacco associated lineage (KIRÁLY et al. 2022) and studying the cost of sexual reproduction (KOBAYASHI and HASEGAWA 2016).

2.13. Sexual differences

Adult sexual dimorphism is a very common phenomenon in thrips species and can be visually determined with the naked eye, but examination with a microscope is sometimes necessary. The sexual differences are more obvious in the suborder Terebrantia than in Tubulifera. In *T. tabaci,* adult males are smaller than females and usually paler in colour than females. They have an elongated, almost parallel-sided abdomen that is bluntly rounded at the tip. The females have a conspicuous, saw-like ovipositor, which usually lies retracted beneath a gradually tapered abdomen (LEWIS 1973).

2.14. Identification of sex in larval stages

In the family Thripidae, the sex of first and second-instar larvae can be distinguished by a different number of setae on abdominal segment IX. Females and males of the first instar larvae have three and four pairs of setae on the abdominal segment IX, respectively. There is only one pair of ventral setae in the females of the first instar larvae and two pairs of dorsal setae. In the males of the first instar larvae, there are two pairs of ventral setae and two pairs of dorsal setae. In the second instar, females and males have four and five pairs of setae on abdominal segment IX, respectively. Two on the ventral side and two on the dorsal side in female larvae. The second-instar male larvae have five pairs of setae. The ventral aspect has three pairs of setae and the dorsal aspect has two pairs (VIERBERGEN et al. 2010).

2.15. *Thrips tabaci* species complex

2.15.1. Identification of *T. tabaci* lineages based on molecular methods

T. tabaci was considered a single cosmopolitan and polyphagous thrips species until ZAWIRSKA (1976) proposed two different biological types: the communis type and the tabaci type. She observed differences in the range of the host plant, distinct reproductive modes, the capability of transmitting plant viruses (TSWV), and a single morphological difference in the second instar larvae. After that, several molecular genetic studies indicated considerable differences between populations of *T. tabaci* (KLEIN and GAFNI 1996, KRAUS et al. 1999, JENSER et al. 2001). The presence of a cryptic species complex did not find any acceptance until BRUNNER et al. (2004) analysed partial sequences of the Mitochondrial Cytochrome c Oxidase subunit I (COI) gene from populations collected from leek and tobacco crops and divided the species into three lineages based on the host association: leek-associated 1 (L1), leek-associated 2 (L2) and tobacco-associated (T) lineages. Since then, several studies have confirmed the genetic divergence of *T.tabaci* populations (TODA and

MURAI 2007, KOBAYASHI and HASEGAWA 2012, JACOBSON et al. 2013, KOBAYASHI et al. 2013, WESTMORE et al. 2013, LI et al. 2015, SOJNÓCZKI et al. 2015, JACOBSON et al. 2016). Distinguishing the currently known lineages in the *T. tabaci* cryptic species complex required the sequencing of mtCOI fragments. FARKAS et al. (2020) published a simple molecular method for the identification of the *T. tabaci* lineages. The method describes a CASP marker system for distinguishing mtCOI gene sequences of *T. tabaci* lineages and was employed to genotype 116 *T. tabaci* specimens from Hungary. The genetic diversity of onion thrips affects host plant selection, the effectiveness of virus transmission, and insecticide resistance. All of this may pose a biosecurity risk to the countries where the onion thrips are found, but not every genotype of it is established.

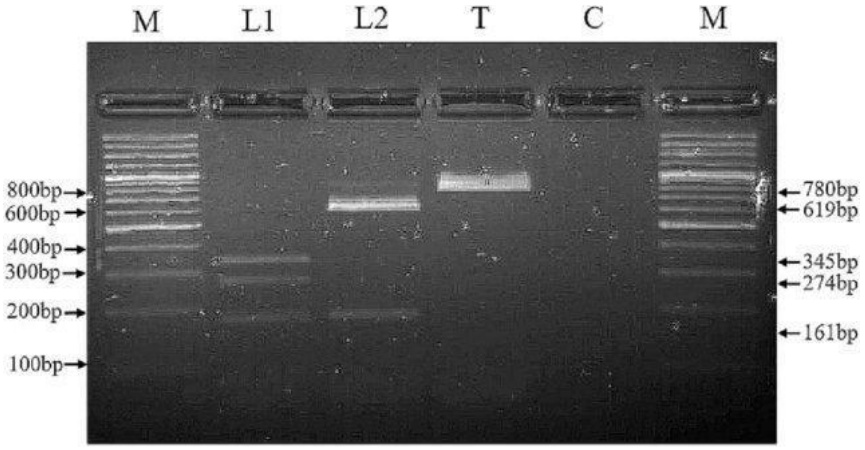


Figure 1. Restriction fragment patterns of the amplified mtCOI gene of *T. tabaci* digested with PsuI and PsyI endonucleases (FARKAS et al. 2020). Lane M is a 100 bp DNA ladder-size marker. L1: three fragments of leek-associated arrhenotokous lineage after digestion (345 bp/274 bp/161 bp), L2: two fragments of leek-associated thelytokous lineage after digestion (619 bp/161 bp), T: undigested amplicon of tobacco-associated arrhenotokous lineage (780bp); C: Negative control with no template DNA.

2.15.2. Morphological variation in the *T. tabaci* species complex

To date, the only accurate method for identifying the lineages of *T. tabaci* is based on molecular techniques. There is no morphological character that could be used to easily distinguish the adults of the *T. tabaci* lineages (JENSER and SZÉNÁSI 2004, KOBAYASHI and HASEGAWA 2012). The morphological dissimilarity between larvae of different species is frequently greater than that between adult thrips (KUCHARCZYK 2010). ZAWIRSKA (1976) observed a single morphological difference in second instar larvae of tobacco and communis types; the posteromarginal

comb on abdominal tergite IX was present in the communis type and absent in the tabaci type. She also observed that the size of the setae on the posterior angle of the prothorax of the communis type is larger compared to the tabaci type. FEKRAT et al. (2014) observed morphological differences between tobacco-associated and onion-associated individuals using morphometric analyses between populations collected on tobacco and onion fields in Iran. However, no external morphological characteristics can provide a morphological distinction between adults of the different lineages of *T. tabaci* were identified. Morphometric measurements are widely used to discriminate between species, especially for cryptic species that are not easily distinguished due to a lack of diagnostic characteristics (NAVIA et al. 2015). Different morphological analyses conducted on different insect groups could distinguish and discriminate the species based on morphometric analyses and geometric morphometrics. Few morphometric studies have been conducted on thrips throughout the world. Based on morphometric analyses of the *Thrips hawaiiensis* (Morgan) species group, two distinct groups corresponding to *T. hawaiiensis* and *T. florum* Schmutz were found throughout the Oriental, Pacific, and American regions, with an intermediate group, *T. exilicornis* Hood, representing the African populations (PALMER and WETTON 1987). Morphometric analyses of *Scirtothrips dorsalis* Hood populations from five continents, including Israel, Japan, India, Florida, and St. Vincent, revealed that populations from Japan differed significantly from four other populations in two or five morphological characters, depending on the populations (KUMAR et al. 2011). TIMMANNA et al. (2021) carried out a morphometric analysis of the sugarcane thrips *Fulmekiola serrata* Kobus collected from two different host plants, suggesting that the population of *F. serrata* collected on sugarcane differs from the population on *Ficus* in body length and antennal length. A geometric morphometric method has been carried out to discriminate against the cryptic species of malaria vector mosquitoes in Western Thailand. In *Anopheles minimus* Theobald 1991 and *A. harrisoni* Harbach & Manguin, belonging to the same cryptic species, wing venation geometry can be used to distinguish between these cryptic species mainly based on shape divergence (CHATPIYAPHAT et al. 2020).

2.16. Life history

2.16.1. Developmental parameters of *T. tabaci* lineages on different host plants and temperatures

Knowing the biology of an insect pest is very important, especially in developing control strategies for future Integrated Pest Management (IPM) programs. Host plants and temperatures play

an important role in affecting insect development and reproduction. Understanding the host plant's preference is very important for pest control. A few studies were conducted to study the biological parameters of *T. tabaci* in relation to the host plant. The majority of studies reported information on *T. tabaci* life table parameters from a single host plant, and only a few studies compared them in different host plants, but due to a lack of data, it is impossible to determine which lineage they tested. Most of the data available is from the L2 lineage (SALAS 1994, VAN RIJN et al. 1995, SALMASI et al. 2003, ARRIECHE et al. 2006, POURIAN et al. 2009, PATEL et al. 2013, LI et al. 2014, MORAIET et al. 2017, BASRI et al. 2019, DEVI and ROY 2019, MIRI et al. 2021). In all of these studies, no males were reported. So far, only a few studies have compared the developmental time of *T. tabaci* in the different host plants; onion and tobacco (FEKRAT et al.2009); onion and cabbage (LI et al. 2014); cabbage, garlic, and onion (BASRI et al. 2019); lentil and chickpea (MIRI et al. 2021). From these studies, only LI et al. (2014) compared the developmental parameters of the two identified L1 and L2 lineages of *T. tabaci* based on their reproductive mode and mtCOI gene (L1 and L2). In this study, the performance of L1 and L2 lineages was different in the two host plants. On onion, the development of first and second instar larvae, prepupa, and pupa in the L2 lineage of *T. tabaci* was slower compared with the L1 lineage. Moreover, the L2 lineage of *T. tabaci* had lower total and daily fecundity. The opposite results were found in cabbage (LI et al. 2014). BASRI et al. (2014) concluded that garlic caused a reduction in pupal development, longevity, and fecundity. According to MIRI et al. (2021), lentil is the more suitable host plant for onion thrips when compared to chickpea. Table 3 and 4 show the mean duration of the life cycle, as well as preoviposition, fecundity, and longevity of *T. tabaci* on various food sources and temperatures. These data indicate that besides temperature the host plant is also an important factor influencing the development of *T. tabaci*.

Table 3. Mean duration (in days ± SD) of different developmental stages of *Thrips tabaci* according to temperature and food. Food source: O-onion, C- cucumber, T-tobacco, H-P honey and pollen, G-garlic, E-S EmiliaSagitatta, Ca-canola, L-lentil, Ch- chickpea.

Lineage	**Food**	**Temp**	**Developmental parameters**						**References**
			Egg	1st larva	2nd larva	Prepupa	Pupa	Egg to adult	
L2	C	25	3.92±0.32	2.13±0.45	3.17±0.45	1.09±0.23	2.43±0.23	12.90±0.89	VAN RIJN et al. 1995
L2	C	25	2.82±1.33	1.95±1.42	4.12±0.92	1.03±1.44	1.97±0.91	14.40±3.13	POURIAN et al. 2009
L2	O	27	4.18±0.53	2.08±0.56	2.11±0.80	1.25±0.80	1.25±0.47		SALMASI et al. 2003
L2	O	23.4	3.2±0.52	2.7±0.21	2.9±0.18	1.9±0.33	3.5±0.45	14.2±1.7	ARRIECHE et al. 2006
L2	O	32.04	4.33±0.61	2.09±0.53	2.04±0.53	1.17±0.31	2.40±0.52		SALAS 1994

T	T	25±2	5.11±0.07	2.71±0.08	3.88±0.07	2.61±0.05	3.68±0.09	17.82±0.17	FEKRAT et al. 2009
L1	O	20±1	6.6±0.03	2.9±0.04	4.4±0.09	1.6±0.03	3.6±0.03	18.9±0.12	LI et al. 2014
L1	C	20±1	6.5±0.47	2.9±0.45	3.7±0.10	1.6±0.02	3.4±0.03	18.0±0.13	
L2	O	20±1	6.7±0.04	3.2±0.05	5.5±0.15	1.9±0.05	3.8±0.06	20.7±0.23	
L2	C	20±1	6.5±0.53	2.8±0.40	3.6±0.06	1.5±0.02	3.5±0.02	17.8±0.10	
L2	H-P	15	11.41±0.91	7.15±1.46	9.56±1.89	3.53±0.69	7.89±0.56		MURAI 2000
L2	H-P	20	6.53±0.59	3.26±0.55	3.92±0.54	1.89±0.39	3.95±0.27		
L2	H-P	23	5.03±0.51	2.80±0.41	3.26±0.45	1.17±0.37	3.22±0.55		
L2	H-P	25	4.99±0.41	2.38±0.54	2.87±0.57	1.11±0.31	2.63±0.56		
L2	H-P	30	3.76±0.44	1.85±0.17	1.89±0.46	0.80±0.25	2.33±0.48		
L2	O	25±1	4.12±0.18	2.50±0.11	2.76±0.16	1.41±0.10	1.54±0.10		MORAIET et al. 2017
L2	O	25±1	5.06±0.17	1.89±0.10	3.00±0.16	1.21±0.06	1.69±0.08		
L2	O	25±1	2.16±0.11	1.86±0.09	2.42±0.11	1.70±0.10	1.45±0.12		
L2	O	25±1	3.68±0.10	1.83±0.09	1.79±0.11	1.71±0.11	1.62±0.08		
L2	C	22±1	5.46±0.28	3.88±0.11	3.58±0.08	3.48±0.08	3.18±0.09	19.63±0.36	BASRI et al. 2019
L2	G	22±1	5.96±0.11	3.92±0.08	3.14±0.1	2.1±0.09	2.21±0.1	17.32±0.29	
L2	O	22±1	5.7±0.1	2.32±0.07	2.8±0.07	2.32±0.08	2.24±0.1	15.37±0.21	
L2	O	22±1	6.46±0.11	2.72±0.06	2.93±0.09	3.23±0.09	2.38±0.08	17.76±0.18	
L2	E-S	24.75	4.19	7.66		1.50	2.80	16.15	SAKIMURA 1932
L2	E-S	23.48	4.55	9.08		1.66	2.87	18.16	
L2	E-S	22.38	4.85	9.26		1.55	3.52	19.18	
L2	E-S	22.44	4.82	9.54		1.42	3.53	19.31	
L2	O		3.6	6.4		1.2	3.2	10.8	SAKIMURA 1937
L2	O		5.6	8.6		2.0	4.2	14.8	
L2	O		6.5	13.5		2.8	6.3	22.7	
L2	O	15.8	8.5	6.5		2.0	4.0	21.0	LALL and SINGH 1968
L2	O	18.0	7.9	6.2		2.0	3.5	19.0	
L2	O	23.4	6.0	5.5		1.7	2.8	16.0	
L2	O	30.8	4.8	5.3		1.4	2.4	13.9	
L2	O	27±2	2.90±1.38	2.33±0.53	4.62±0.76	2.10±0.38	3.78±1.00	16.38±1.99	DEVI and ROY 2019
L2	C	15	9.68±0.02	5.47±0.02	9.31±0.02	2.85±0.01	5.45±0.02	32.76±0.04	DELIGEORGIDIS et al. 2006
L2	C	20	5.93±0.01	2.95±0.01	5.03±0.01	1.94±0.01	3.38±0.03	19.23±0.03	
L2	C	25	5.12±0.01	1.91±0.01	4.02±0.01	1.59±0.02	3.01±0.01	15.65±0.02	
L2	C	30	3.99±0.01	1.07±0.01	3.92±0.01	1.04±0.01	1.76±0.02	11.78±0.02	
L2	O	25±1	4.52±0.51	2.52±0.51	3.41±0.50	1.96±0.76	3.56±0.50	17.29±1.55	PATEL et al. 2013
L2	Ca	25±1	3.92±0.20	6.53±0.32		5.13±0.26		15.58±0.32	FATHI et al. 2011
L2	Ca	25±1	3.80±0.20	5.13±0.32		4.66±0.25		13.59±0.39	
L2	Ca	25±1	4.40±0.13	6.33±0.38		5.13±0.25		15.86±0.31	
L2	Ca	25±1	4.73±0.15	6.87±0.29		5.27±0.25		16.87±0.36	
L2	Ca	25±1	4.26±0.12	4.86±0.32		4.66±0.24		13.78±0.34	
L2	Ca	25±1	3.73±0.12	4.06±0.32		4.46±0.21		12.25±0.26	

L2	L	25±1	2.93±0.08	2.47±0.06	3.29±0.1	1.72±0.06	3.38±0.07	13.81±0.16	MIRI et al. 2021
L2	Ch	25±1	3.19±0.09	2.96±0.09	3.82±0.11	2.15±0.07	3.68±0.1	15.81±0.16	

Table 4. Mean duration (± SD) of preovipostion and adult longevity (in days), daily, and total fecundity of *Thrips tabaci* according to the host plant and temperature. Food source: C- cucumber, O- onion, T-tobacco, G- garlic, H-P honey and pollen, E-S Emilia Sagittata, Ca- canola, L-lentil, Ch-Chickpea.

Lineage	**Food**	**Temp**					**References**
			Preoviposition	Daily fecundity	Total fecundity	Longevity	
L2	C	25	1.90±0.26	-	27.5	11.9	VAN RIJN et al. 1995
L2	O	27	3.60±1.28	2.04±0.84	31.63±18.86	16.15±7.58	SALMASI et al. 2003
L2	O	23.4	2.0	-	39±10.5	11.5±1.8	ARRIECHE et al. 2006
L2	O	32.4	2.7±1.26	1.9±0.56	37.0±9.83	21.5±3.69	SALAS 1994
L2	O	15.8			49.8	18.8	LALL and SINGH 1968
L2	O	18.0			51.7	19.6	
L2	O	23.4			55.0	20.1	
L2	O	30.8			28.2	20.2	
L2	C	25±1			26.82±5.56	12-17	POURIAN et al. 2009
L2	H-P	15	8.64±0.56		169.6±94.2	86.6±36.6	MURAI 2000
L2	H-P	20	4.37±0.56		210.0±148.9	46.8±21.4	
L2	H-P	23	3.41±0.71		270.4±111.6	41.7±14.5	
L2	H-P	25	2.35±0.56		165.0±84.8	25.0±10.2	
L2	H-P	30	1.96±0.64		62.6±35.9	12.8±4.6	
L2	O		1.54±0.10	3.89±0.18	67.22±3.74	19.22±0.86	MORAIET et al. 2017
L2	O		1.69±0.13	3.93±0.20	83.81±4.54	22.39±0.92	
L2	O		1.29±0.11	3.76±0.24	33.94±3.38	5.97±0.92	
L2	O		2.00±0.15	3.49±0.24	27.12±3.30	5.29±0.84	
T	T	25±2	2.50±0.25	1.41±0.11	26.35±1.93	19.07±1.51	FEKRAT et al. 2009
L1	O	20±1		3.4±0.2	118.7±11.0	29.8±1.9	LI et al. 2014
L1	C	20±1		2.3±0.1	84.9±6.1	38.3±3.0	
L2	O	20±1		2.4±0.2	84.9±10.0	28.7±2.4	
L2	C	20±1		3.2±0.2	113.6±8.4	35.7±2.2	
L2	C	22±1	3.8±0.25	3.39±0.13	80.4±2.62	30.7±0.96	BASRI et al. 2019
L2	G	22±1	2.5±0.17	3.1±0.11	58±3.09	23±0.71	
L2	O	22±1	4.5±0.17	3.34±0.08	78±2.14	30.2±0.74	
L2	O	22±1	4.1±0.18	3.27±0.05	75.4±1.56	29.5±0.45	

L1	C	15	5.47±4.89		19.88±12.65	34.22±9.88	WOLDEMELAK et al. 2021
L1	C	23	2.08±0.88		107.63±74.15	24.64±12.28	
L1	C	30	1.00±0.00		74.78±29.47	13.63±5.45	
T	T	15	11.31±3.37		70.82±38.48	81.82±15.26	
T	T	23	1.89±1.11		84.83±28.57	26.20±5.27	
T	T	30	1.31±0.60		58.33±21.40	13.91±3.88	
L2	E-S	24.98	4.8	2.5	34.4	21.0	SAKIMURA 1932
L2	E-S	22.28	7	1.6	42.0	40.3	
L2	E-S	22.78	6	1.6	37.5	28.9	
L2	O		2.8		80		SAKIMURA 1937
L2	O		3.9		53.9		
L2	O		2.5		44.8		
L2	O	27±2	2.00±0.76		29.93±9.05	25.38±2.37	DEVI and ROY 2019
L2	C	15	8.06±0.20	0.66±0.02	24.73±0.66	54.12±0.30	DELIGEORGIDIS et al. 2006
L2	C	20	2.60±0.12	1.72±0.04	53.33±1.40	38.26±0.26	
L2	C	25	2.26±0.11	1.74±0.04	39.93±1.32	27.25±0.24	
L2	C	30	2.13±0.09	1.61±0.03	28.46±1.72	20.99±0.19	
L2	O	25±1	3.43±1.10		56.63±11.73	27.97±6.01	PATEL et al. 2013
L2	Ca	25±1			18.86±0.96	16.40±0.61	FATHI et al. 2011
L2	Ca	25±1			33.00±1.09	18.40±0.54	
L2	Ca	25±1			25.80±1.09	16.47±0.52	
L2	Ca	25±1			15.53±0.58	15.13±0.36	
L2	Ca	25±1			41.93±2.00	22.27±1.23	
L2	Ca	25±1			44.06±5.16	25.27±1.23	
L2	L	25±1	1.25±0.05		43.90±0.95	13.44±0.16	MIRI et al. 2021
L2	Ch	25±1	2±0.07		24.84±0.68	13.91±0.17	

Temperature is one of the most important environmental factors that influence the colonization, distribution, abundance, behaviour, life history, and fitness of insects. Like other insect species, *T. tabaci* is an ectothermic insect species, which means it is unable to control its body temperature, which changes with fluctuations in the ambient temperature. In several studies on onion thrips, the effect of temperature has shown that there is a log-linear relationship between developmental time, preoviposition, fecundity, egg hatchability, and longevity (FEKRAT 2009, MURAI 2000). Higher temperatures subsequently reduce the reproductive fitness of thrips species. The fecundity reduction of *T. tabaci* reared on honey and pollen was observed at 30°C, but the highest was at 23°C at 270 eggs per female (MURAI 2000). As a result, only species that can adapt quickly

and efficiently to temperature change can survive (MERENE 2015). The effect of temperature on the development of *T. tabaci* as a single species has been investigated in several studies (EDELSON and MAGARO 1988, MURAI 2000, POURIAN et al. 2009). Development increases with temperature, but there is an upper-temperature limit, above which the animal can no longer develop, and a lower temperature limit, below which development stops. The optimum temperature of *T. tabaci* was 23°C (MURAI 2000). The development time at this temperature is about 15 days from egg to adult. EDELSON and MAGARO (1988) presented a lower temperature limit of 11.5º C. The sex ratio of males and females and the life table parameters of L1 and T lineages of *T. tabaci* at different temperature levels have recently been studied (WOLDEMELAK et al. 2021). Based on this study, the optimal temperature level for the reproduction of *T. tabaci* lineages is 23°C. Temperature affected all life table parameters of the L1 and T lineages. The proportion of males and females was also affected by the temperature. The proportion of females increased log linearly as the temperature increased. The preoviposition period, fecundity, egg hatchability, and adult longevity were reduced as the temperature increased. Moreover, WOLDEMELAK et al. (2021) indicated that the T lineage has much better tolerance to lower temperatures than the L1 lineage, regarding fecundity at 15 and 23ºC. Understanding the effects of different temperatures on reproduction and development is essential for understanding the life history and population dynamics of this pest.

2.16.2. Sex ratio

Thrips tabaci populations exhibit a female-biased sex ratio (LEWIS 1973). However, the ratio of males to females varies depending on the host plant, regions, latitudes, and seasons (KENDALL and CAPINERA1990, JENSER et al. 2006), and more recently, TSWV has been reported to modulate the sex ratio in western flower thrips *Frankliniella occidentalis* by down-regulating an FSCB-like gene (TAO et al. 2022). The majority of *T. tabaci* populations propagate by parthenogenesis. The occurrence of males is rather diverse within the geographical distribution. In the Eastern Mediterranean region, males were collected in large numbers from *Allium*, which is believed to be the primary breeding plant (MOUND 1992). Males are rare or absent in other parts of the worlds. In Hungary, only females were observed among a large number of specimens of cabbage (*Brassica oleracea*) (FAIL and PÉNZES 2004). Males were not present in numerous plant species in the ruderal vegetation and Hungarian National Parks. At the same time, males were observed above all in the cultivated plants such as tobacco (*Nicotiana tabacum),* onion (*Allium cepa*), and potato (*Solanum tuberosum*) and some weed plants like *Galinsoga parviflora*, *Stellaria media*, and *Datura*

stramonium. During the vegetation period, the sex ratio of males to females and the individual number of males changed (JENSER et al. 2006). Sex ratios vary among the population of sexual strain (KOBAYASHI and HASEGAWA 2012, KOBAYASHI et al. 2013). The sex ratio in the arrhenotokous strain was highly female-biased in an onion population in Hokkaido (3 males and 47 females) (KOBAYASHI and HASEGAWA 2012). KENDALL and CAPINERA (1990) reported a sex ratio of 1 male to 6 females in onion populations in Colorado. In the Netherlands, the sex ratio was 1 male to 25 females (VIERBERGEN and ESTER 2000). In Iowa, the sex ratio was 1 male to 10 females (HARRIS et al. 1936). There was 1 male to 113 females in Michigan (SHULL 1914). On garlic, leek, and onion in Central Spain, 1 male and 2 females (TORRES VILA et al. 1994). There was one male and 300 females in Sudan (MCGILL 1927 cit. LEWIS 1973). In Italy, the sex ratio in an open field of eggplant was highly female-biased, with male numbers low in the spring and summer, while female numbers were higher in the late spring and full summer. In the leek plant, males were reported in the field, but no males were reported in the laboratory experiment (MARULLO and DE GRACIE 2012). In Lithuania, males were not found in two years of research (2002 and 2003) in winter rye (*Secale cerale*) and winter wheat (*Triticum aestivum* L), while the females were present in both years (ŠMATAS 2009, ŠMATAS et al. 2013). Within three vegetation seasons (2014-2016), the sex ratios on one cultivar of Welsh Onion (*Allium fistulosum* L.) and eight cultivars of onion (*Allium cepa* L.) in South Poland were highly biased toward females, ranging from 99.8% to 100%. (OLCZYK and POBOŻNIAK 2020).

2.16.3. Oviposition behaviour

Thrips of the Terebrantia suborder lay their eggs singly in an incision made in the plant tissue by their ovipositor. The part of the plant chosen differs between species. Females of *T. tabaci* lay their eggs indiscriminately in the leaves, petals, cotyledons, sepals, or glumes (LEWIS 1973). LEWIS (1973) and TERRY (1997) described a sequence of oviposition behaviour that is assumed to be typical of most Thripidae. Before egg-laying, the female contracts her abdomen, pushing the egg down to the oviduct. The tip of the abdomen is then arched toward the plant surface and the long sensory terminal setae search for a suitable site for egg-laying. This latter behaviour was observed in *T. tabaci* by RIEFLER and KOSCHIER (2009) and was named “abdomen dragging”. Based on their study, it occurred not only before egg deposition but more often before other behavioural elements related to explorative behaviour. As a result, the authors attributed only the contractions of the abdomen and

pushes that indicate the ovipositor pierces the plant tissue, whereas LEWIS (1973) attributed a movement sequence during oviposition to the number of eggs laid.

2.16.4. Feeding

T. tabaci feeds uniquely by punching through the leaf surface and extracting sap from plant cells. During feeding, thrips release substances that help predigest tissue. After that, they siphoned off the contents of mesophyll cells, which ultimately depleted chlorophyll on leaves and reduced the phytochemical efficiency (BOATENG et al. 2014). Because of that, the damage appears as silvery leaf spots that later develop into blotches. The blotches develop in the silvery patches or streaks on the leaves (RUEDA and SHELTON 1995, CRASHNAW 2008). Morphological plant characteristics and primary and secondary plant metabolites are known to determine the acceptability of a plant as a host (ANANTHAKRISHNAN and GOPICHANDRAN 1993), which may affect the behaviour of thrips in different plants. Plant morphological characteristics such as leaf hairs and wax layers are known to determine the suitability of cotton (RUMMEL and QUISENBERRY 1979), garlic (OLIVEIRA and CASTELLANE 1996), and onion (DAMON et al. 2014) for feeding. Moreover, primary metabolites such as proteins, sugars, and carbohydrates stimulate the feeding of thrips (MOLLEMA and COLE 1996, BRODBECK et al. 2001). Observations of the feeding behaviour of *T.tabaci* have been described by RIEFLER and KOSCHIER (2009). Based on their observations, feeding behaviour is described as continued pumping movements of the head more than five times, together with the back-and-forth movement of the body (RIEFLER and KOSCHIER 2009*). T. tabaci*'s continued penetrations of parenchyma cells can be seen as a continuous oscillating movement of the heads under the microscope (HARREWIJN et al. 1996). *T. tabaci* females on cucumber began sustained feeding shortly after their release on plant tissue and within 24 hours they spent more time feeding on a cucumber than on leeks, according to RiEFLER and KOSCHIER (2009). As a result, larger areas showing silver damage were measured in cucumber. Thrips feeding on the spongy parenchyma cells on the dicotyledonous cucumber's abaxial leaf surface may differ from those feeding on the palisade parenchyma of the monocotyledonous leek. It can be seen that dissimilarities between plants play a decisive role in the feeding behaviour of onion thrips.

2.16.5. Overwintering

Most records of overwintering *T. tabaci* are of adults (LEWIS 1973). Knowledge of the overwintering locations and subsequent dispersal of *T. tabaci* is very important for designing control strategies. There are few studies published regarding the overwintering sites of *T. tabaci* that include

sampling in the fields during winter, and those that do exist focus on the crop plants. *T. tabaci* adults were collected from alfalfa (*Medicago sativa* L.), clover (*Trifolium pratense* L.), grass sod, and onions during the winters of 1945-1950 in Idaho (SHIRCK 1951). During the winters of 1952-1953, *T. tabaci* were found on alfalfa, red clover, winter wheat (*Triticum aestivum* L.), and oat (*Avena sativa* L.) in Canada (BOYCE and MILLER 1953). It was also reported that onion thrips can successfully overwinter within winter wheat, *Triticum aestivum*; alfalfa, *Medicago sativa;* and weed vegetation in New York during the winters of 1982-1983 and 1983-1984. The overwintering females were capable of oviposition on these plants in spring and reproduction (NORTH and SHELTON 1986). After the emergence of the winter wheat in September or October, females enter the fields and overwinter there. They may already be present in the winter wheat, alfalfa, and weedy vegetation or move into ditches from the cabbage fields. LARENTZAKI et al. (2007) reported that overwintering locations of *T. tabaci* in the onion cropping ecosystem in New York are in the soil, within and near onion fields; they can also survive in the volunteer onions and weeds after onions are harvested. These volunteers offer overwintering sites for early-season feeding before the onion crop emerges in the spring and after it is harvested in the fall. Among the voluntary weeds that adult *T. tabaci* can colonize late in the fall are, in particular, pigweed, *Amaranthus hybridus* L. and lambs quarters, *Chenopodium album* L. In South Auckland, it was reported that onion thrips bred in the "wild" self-set plants, sprouted bulbs, and destroyed crops during the winter of 1999 (MARTIN 2014). Consequently, management strategies against *T. tabaci* should include tactics that reduce volunteer onion and weed abundance.

2.17. Characterization and specificity of *T. tabaci* in the transmission of plant viruses

Besides causing direct damage to the plants, *T. tabaci* is known for transmitting plant ortho-tospoviruses, namely, Tomato spotted wilt virus (CHATZIVASSILIOU et al. 2002), Iris yellow spot virus (BAG et al. 2015), Tomato yellow ring virus (RASOULPOUR and IZADPANAH 2007) and Alstroemeria yellow spot virus (HASSANI-MEHRABAN et al. 2019). It is one of 14 known thrips species that are vectors of ortho-tospoviruses (RILEY et al. 2011, ROTENBERG and WHITFIELD 2018). Twenty ortho-tospovirus species have been identified globally, with 14 thrips species in the family Thripidae that can transmit the viruses (ULLMAN et al. 1997, JONES 2005, PAPPU et al. 2009, CIUFFO et al. 2010, HASSANI-MEHRABAN et al. 2010). Before 2017, orthotospoviruses were considered to be part of the genus Tospovirus in the family Bunyaviridae (CHEN et al. 2012 and 2016). However, in 2020, the International Committee on Taxonomy of Viruses (ICTV) announced that the genus Orthotospovirus belongs to the family Tospoviridae (HONG et al. 2021).

Thrips-transmitted ortho-tospoviruses are a major group of plant viruses with a wide host range. A single ortho-tospovirus, Tomato spotted wilt virus (TSWV) has at least 1090 host plant species belonging to 15 families of monocotyledonous plants and 69 families of dicotyledonous plants worldwide (PARRELA et al. 2003). Orthotospoviruses are persistently transmitted by thrips, which means that viruses replicate and circulate in their bodies and remain transmitters even after molting during the developmental stages. The transmission of the ortho-tospoviruses depends on the thrips' ontogeny (MORITZ et al. 2004a). The first instar larva is the most important stage for virus acquisition for subsequent transmission by adults (MORITZ et al. 2004a, WHITFIELD et al. 2005). Transmission studies that have shown variation in the competence of *T. tabaci* as a vector of TSWV are described in the section when we spoke about the known biological and ecological differences of the *T. tabaci* lineages.

2.18. Characterization of resistance to insecticide in *T.tabaci*

One of the several management strategies against *T. tabaci* is the use of pesticides. However, the cryptic nature, high reproductive capacity, overlapping generations, short generation time, and hidden lifestyle make it harder to control (SHELTON et al. 2003, SHELTON et al. 2006, NAULT and SHELTON 2010). Sometimes several applications of insecticides are required for better control of *T. tabaci.* Due to their excessive usage, *T.tabaci* populations in many geographical regions, such as the USA (SHELTON et al. 2003, SHELTON et al. 2006, ADESANYA et al. 2020), Australia (HERRON et al. 2008, HERRON et al. 2011), Japan (MORISHITA 2008, TODA and MORISHITA 2009, AIZAWA et al. 2016), United Kingdom (FOSTER et al. 2010), New Zeland (MARTIN et al. 2003), Izrael (LEBEDEV et al. 2012, ROSEN et al. 2021), Iran (NAZEMI et al. 2015), Nicaragua (RUEDA and SHELTON 2003), Canada (MACINTYRE ALLEN et al. 2005) have developed insecticide resistance. Numerous studies have addressed the underlying mechanisms that govern the development of insecticide resistance in insects (WANG et al. 2022). Some studies have shown that gene mutations can decrease the sensitivity of the target site and thus be responsible for increasing insecticide resistance (DONG 2007, XU et al. 2011, TMIMI et al. 2018, ZEIDABADINEZHAD et al. 2019), while others reported that overexpression of the detoxification gene is the most important mechanism leading to the development of insecticide resistance (XU et al. 2016, FENG et al. 2018, JIN et al. 2019). However, it is agreed that both mechanisms are involved in the development of insecticide resistance. In most of the listed literature, the resistance to a given active ingredient, mainly from the group of organophosphates and pyrethroids is recognized, but the mechanism of the

resistance in most of them has not been reported. To develop a sustainable, long-term protection program, it is essential to understand the mechanisms of insecticide resistance at the molecular level and clarify which gene is responsible for the development of resistance. Reduced neural sensitivity is one of the widely observed dominant mechanisms for pyrethroid resistance, which was first reported in the KDR-resistant *Musca domestica* L. (SODERLUND and KNIPPLE 2003, SODERLUND 2012). The primary site of pyrethroid action is the voltage-dependent Na channel (SODERLUND and KNIPPLE 2003). FORCOLI et al. (2002) discovered that the para sodium channel gene's amino acid change is linked to insecticide resistance in *Frankliniella occidentalis.* Identification of the genetic basis of resistance to each insecticide is very important for onion thrips management, especially in designing molecular markers for precise resistance monitoring.

3. MATERIALS AND METHODS

3.1. Establishment and maintenance of the laboratory colonies

The three stock cultures of *T. tabaci* of distinct lineages were established during the years 2013-2014 from the different host plants collected from the field in Hungary (FARKAS et al. 2020). The stock colonies of L1, L2, and T lineages were maintained separately in ventilated plastic or glass containers at room temperature at the Department of Entomology, Hungarian University of Agriculture and Life Sciences, Budapest. The thrips in the colonies were reared on the leaves of their preferred host plants. The L1 lineage was reared on leek (*Allium porrum* L.), the L2 lineage on cabbage (*Brassica oleracea* L.), and the T lineage on tobacco (*Nicotiana tabacum* L.) leaves.

3.2. Experimental design

To carry out the experiments, the thrips individuals were collected from the stock colonies of the three lineages. As with all Terebrantia, the eggs of *T. tabaci* are inserted into the leaves; bean leaves (*Phaseolus vulgaris* L) were used for all the treatments to facilitate the careful excavation of the eggs (Figure 2) because bean leaves are soft and allow for easy handling of the eggs. Five groups were organized to test the morphometric variability of egg size, newly hatched first instar larvae and newly emerged adults among the L1, L2, and T lineages. The groups correspond to a) L1 virgin female; b) L1 mated female; c) L2 virgin female; d) T virgin female; and e) T mated female. The morphometric measurements of the eggs, first instar larvae and adults were performed on the progeny of every single group. All the rearing processes were performed in a growth chamber (Peltier-cooled incubator IPP260plus, MemmertGmBH + Co.KG, Schwabach, Germany) under controlled conditions at 23° C with a light and dark photoperiod regime of L16:D8h.

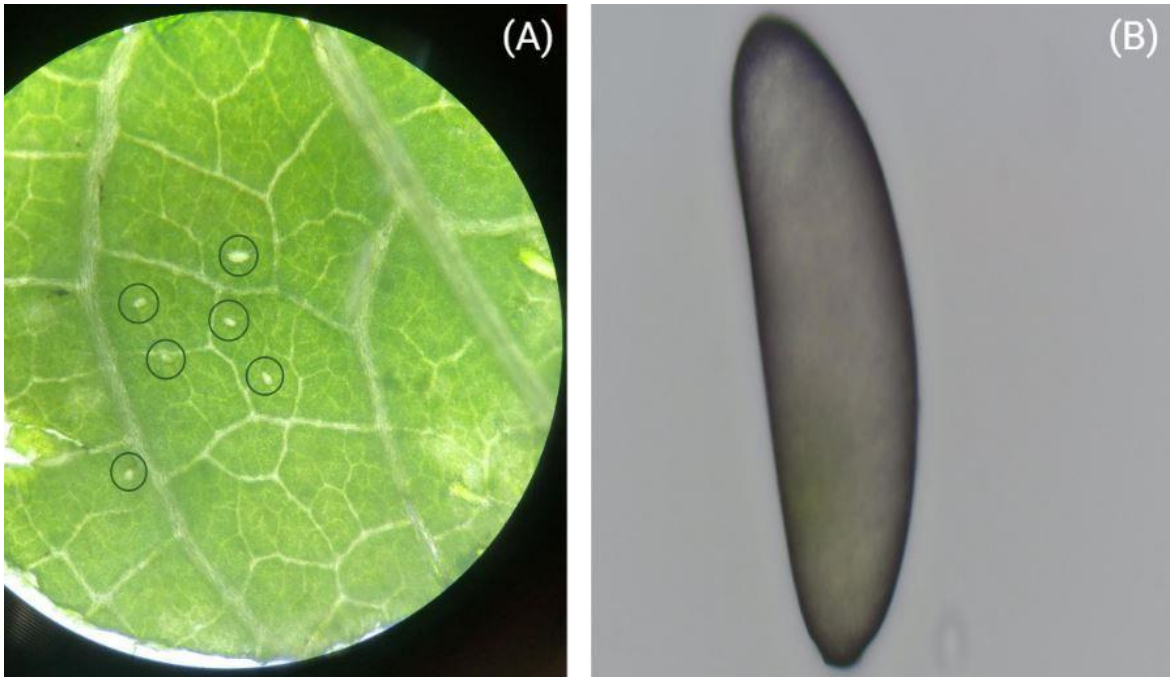


Figure 2. *Thrips tabaci* eggs are inserted into a bean leaf (A) and an egg excavated from plant tissue (B).

3.3. Egg collection from virgin and mated mothers of L1, L2, and T lineages

To measure the size of the eggs produced by virgin and mated mothers of L1, L2, and T lineages, pupae were collected from the stock colonies of *T. tabaci* and isolated separately in a 2 ml Eppendorf tube containing a bean leaf disk to ensure the virginity of the emerging females. Pupae were observed every twelve hours to record the time of adult emergence. From 77 pupae collected from the L1 lineage, 42 females and 15 males emerged. In the case of the T lineage, out of 69 pupae, 45 females and 15 males emerged. In the case of the L2 lineage, 23 females emerged from the 30 pupae collected. Right after adult emergence, 16 females from the L1 lineage and 19 females from the T lineage were accompanied by the emerged males (15 and 21 for the L1 and T lineages, respectively) for mating, one female and one male in each Eppendorf tube containing a bean leaf disk. Each couple was kept together for 48 hours to ensure mating. Then males were removed and preserved in 96% ethanol for DNA-based identification. Meanwhile, the remaining females, of which there were 26 for each of the L1 and T lineages and 23 emerging females from the L2, were kept as virgins. All the virgin and mated females of the three lineages were isolated in a separate Eppendorf tube provided with the bean leaf disk less than 1 cm in diameter for oviposition. Bean leaf disks were changed every twelve hours until the given females died. Under a stereomicroscope (Alpha, NSZ-606, Novel optics, Ningbo Yongxin, Ningbo, China), eggs laid in a bean leaf disk were carefully excavated with the help

of a dissecting needle. In the morphometric analysis of the L1 and T mated groups, only the progeny of those mated females that consisted of both males and females were considered.

3.4. Egg size measurements

The excavated eggs were placed on a microscopic glass slide under a calibrated compound light microscope (LEICA DM LB, Leica Microsystem GmBH, Wetzlar, Germany) with an ocular graticule for the size measurement. Under 600x magnification, eggs were measured for width and length. After the measurements, the eggs were placed back on a new bean leaf disk inside the Eppendorf tube to facilitate hatching and subsequent juvenile development. Eggs were maintained in the controlled environmental conditions described above. As the morphological identification of males and females is not possible in the egg stage, the sex of the resulting offspring was recorded on the slide-mounted specimens of either first instar larvae or newly emerged adults. The eggs were checked every twelve hours for newly hatched larvae. The first instar larvae differ from the second-instar larvae by having six pairs of setae on the pronotum and one pair of sternal setae on abdominal segments IV-VIII. The second instar larvae have seven pairs of setae on the pronotum and three pairs of sternal setae on abdominal segments IV-VIII (VIERBERGEN et al. 2010). Immediately after hatching (maximum 12 hours), about half of the newly hatched larvae was placed in 75% alcohol and preserved at 4°C until the morphometric measurements were processed. While the other portion of the newly hatched first instar larvae were reared on bean leaf disks until they reached the adult stage. The newly emerged adults were also placed in 75% alcohol and preserved at 4°C until they were measured.

3.5. Egg volume

The volume of the eggs was calculated using the formula proposed by CHURCH et al. (2019), which was used to calculate the volume of eggs of a similar shape to *T. tabaci* eggs. Based on this formula, egg volume was calculated from two measured dimensions, namely length and width, assuming that thickness and width are equal:

$$V = \frac{width * thickness * length * \pi}{6} = \frac{width^2 * length * \pi}{6}$$

3.6. Morphometric measurements of first instar larvae and adults of *T.tabaci* lineages

A total of 642 specimens of first instar larvae of the three lineages of *T. tabaci* (212 L1, 88 L2, and 342 T) and 808 specimens of the adult (253 L1, 150 L2, and 405 T) were slide mounted in drops of Berlese mounting medium. The slide-mounted specimens were kept in the oven at 50°C for two days. Then the slide-mounted specimens of first-instar larvae produced by mated mothers of L1 and T lineages were sexed according to VIERBERGEN et al. (2010). All the specimens were measured at 400x and 600x magnification under a calibrated compound microscope (iScope series, Euromex Microscope bv, the Netherlands), with an eyepiece graticule, where the distance between the base of the setae was measured in nine chosen characters for the first instar larvae and eight chosen characters for the adults. The measured characters are illustrated in Figures 3 and 4 and listed in the legend. Larval character state and chaetotaxy are adapted from VIERBERGEN et al. (2010) and SPEYER and PARR (1941). Based on the position of the dorsal setae on the pronotum of the second instar larvae (VIERBERGEN et al. 2010), we think that the missing setae pair in the first instar larva is setae D6. Because of that, we kept numbering the setae pairs according to their position in the second instar larva. Similarly, the position of the ventral setae of the abdominal sternite IX in males and females in the second instar larvae (VIERBERGEN et al. 2010) indicates that the missing pair in the first instar larvae of the female is setae V1, and for males of the first instar larvae, the missing pair is setae V2. Hence, the setae pairs of the first instar larvae are named according to their position in the second instar larvae of both males and females. The morphological terminology of the adults follows PALMER et al. (1992).

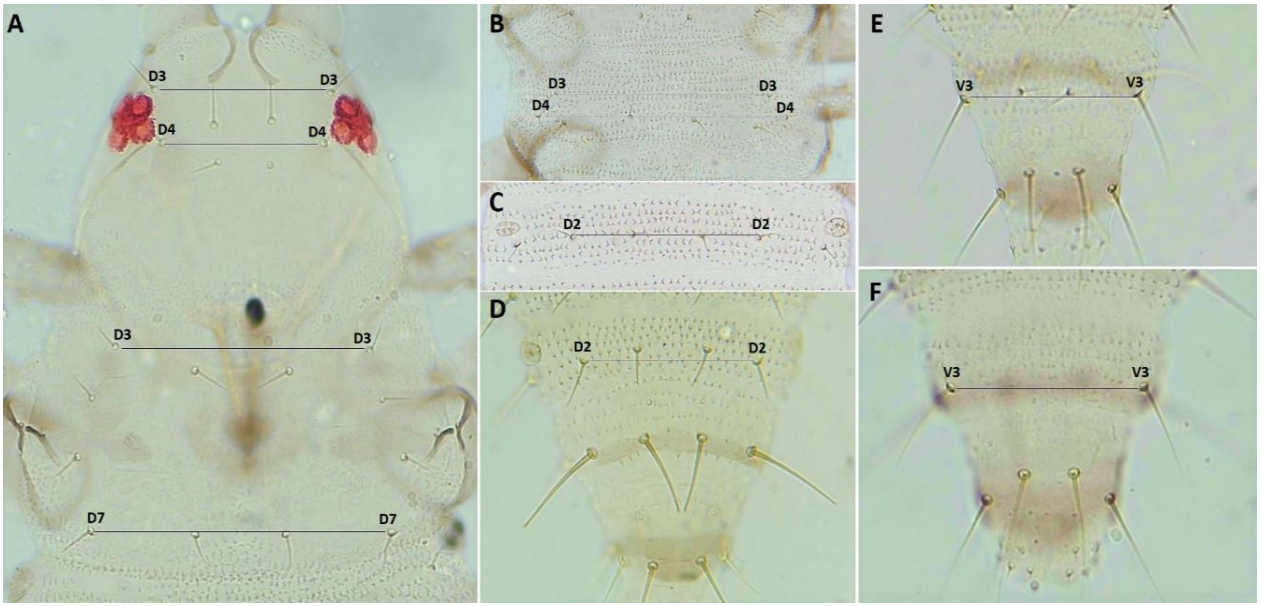


Figure 3. Morphometric measurements of first instar larvae. (A) D3 and D4 head, the distance between dorsal setae three and four of the head; D3 and D7 pronotum, the distance between dorsal setae three and four of the pronotum. (B) D3 and D4 metanotum, the distance between dorsal setae three and four of metanotum. (C) D2 tergite II, the distance between dorsal setae two of abdominal tergite II (D) D2 tergite VIII, the distance between dorsal setae two of abdominal tergite VIII. (E) and (F) V3 sternite IX, the distance between ventral setae three of abdominal sternite IX on a male (E) and a female (F).

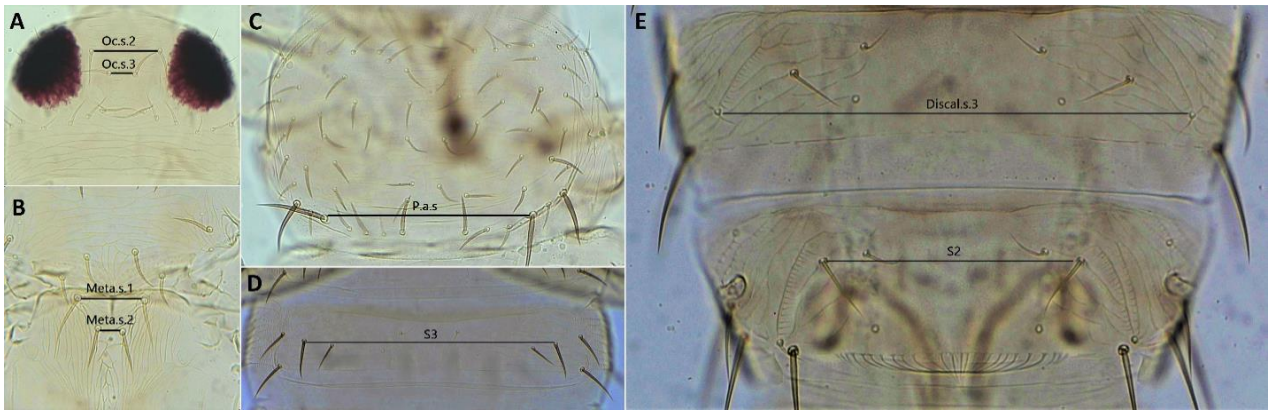


Figure 4. Morphometric measurements of adults. (A) Oc.s.2 and Oc.s.3, the distance between the second and third ocellar setae. (B) Meta.s.1 and Meta.s.2, the distance between lateral and median metanotal setae. (C) P.a.s., the distance between inner posteroangular setae on the pronotum. (D) S3 tergite IV, the distance between dorsal setae three of tergite IV. (E) Discal.s.3, the distance between discal setae three of tergite VII; S2 tergite VIII, the distance between dorsal setae two of tergite VIII.

3.7. *Thrips tabaci* lineage identification

The molecular method of FARKAS et al. (2020) was used to identify all of the females and males whose progeny was used in this study. Briefly, total genomic DNA was extracted from each female and male. The 780bp mitochondrial COI (mtCOI) fragment was then amplified with a specific forward primer (5′-ATTAATTATAGGRCTTTAYAAAGAAGG-3′) and reverse primer (5′-GTAGTGAAAGTGAGCTACAACATAATA-3′). After that, the digestion of the PCR products was facilitated with restriction enzymes (Psul and Psyl). Lineages can be indubitably sequestered by gel electrophoresis since the L1 lineage has two restriction sites for both Psul and Psyl, which results in three different-sized fragments (345 bp, 274 bp, and 161 bp); the L2 lineage has only one restriction site, producing two different fragments (619 bp and 161 bp); and the T lineage does not have restriction sites for either of the two enzymes and remains in a single fragment (sized at 780bp).

3.8. Effect of mating and egg size on the hatching probability of the eggs

To investigate whether egg size is an appropriate predictor of energy content in the L1 and T lineages of *T. tabaci*, we assessed the effect of mating and egg size on the hatching probability of the eggs in the progeny of virgin and mated mothers of the L1 and T lineages. The hatchability of the eggs was recorded as hatched and unhatched for all the eggs laid throughout the entire lifespan of the mothers. The egg hatchability rates were compared between virgin and mated mothers of the L1 and T lineages using the Chi-squared test. While the size of the eggs (width, length, and volume) laid by virgin and mated mothers of the L1 and T lineages was compared using a one-way random block design MANOVA, according to their hatchability (hatched and did not hatched), with the factor "hatchability" and mother ID as a block.

3.9. Egg size and sex allocation

3.9.1. Comparison of male and female egg size produced by mated mothers of the L1 and T lineages

To quantify maternal investment in eggs, we compared the size of eggs in male and female offspring produced by mated mothers during their entire lifespan. In two studied species, *T. urticae* MACKE et al. 2011b) and *P. kellyanus* (KATLAV et al. 2020) egg size and gender were found to be correlated with the egg mass produced by young arrhenotokous females. Corresponding to these approaches, we compared male and female egg sizes in different age groups of the mothers; 3-5 days old (just like *T. urticae*) and 7-10 days old (similar to *P. kellyanus*) and above 10 days old. The

analysis of the egg size (width, length, and volume) of male and female offspring produced by mated mothers of the L1 and T lineages was performed using one-way multivariate analysis of variance (MANOVA) with the factor of 'gender'. We carried out the same analysis for all age groups.

3.9.2. Testing the model of egg size and sex allocation

We investigated whether the asymmetric allocation of male and female eggs by mothers could occur before fertilization and whether egg size influences the probability of an egg being fertilized (a female fertilized egg being larger than a male unfertilized egg) (Figure 5A, scenario 1). Under this scenario, the range of egg size should be similar between virgin and mated mothers. Moreover, any sex-specific differences in egg size would result from the selective fertilization of larger eggs, leading to the larger egg size of males produced by virgins than by mated mothers.

Second, we tested whether mating affects the female resource allocation strategy if eggs draw more resources once they are fertilized, which is also possible because eggs in the majority of insects, including thrips, are fertilized just before the end of vitellogenesis (CHAPMAN 1998) (Figure 5B, scenario 2). Under this scenario, the size of the eggs is expected to be larger among eggs from mated mothers than among virgins, and mating should increase the egg size in general, leading to equal egg size in males and females produced by mated mothers and, therefore, a smaller egg size in males produced by virgin mothers. To discriminate between these two scenarios, we compared the mean and the distribution of the egg size produced by virgin and mated mothers. The analysis of egg size (width, length, and volume) produced by virgin and mated mothers of the L1 and T lineages was performed for the entire lifespan of the mothers and age groups using one-way MANOVA, where the factor was 'mating status'.

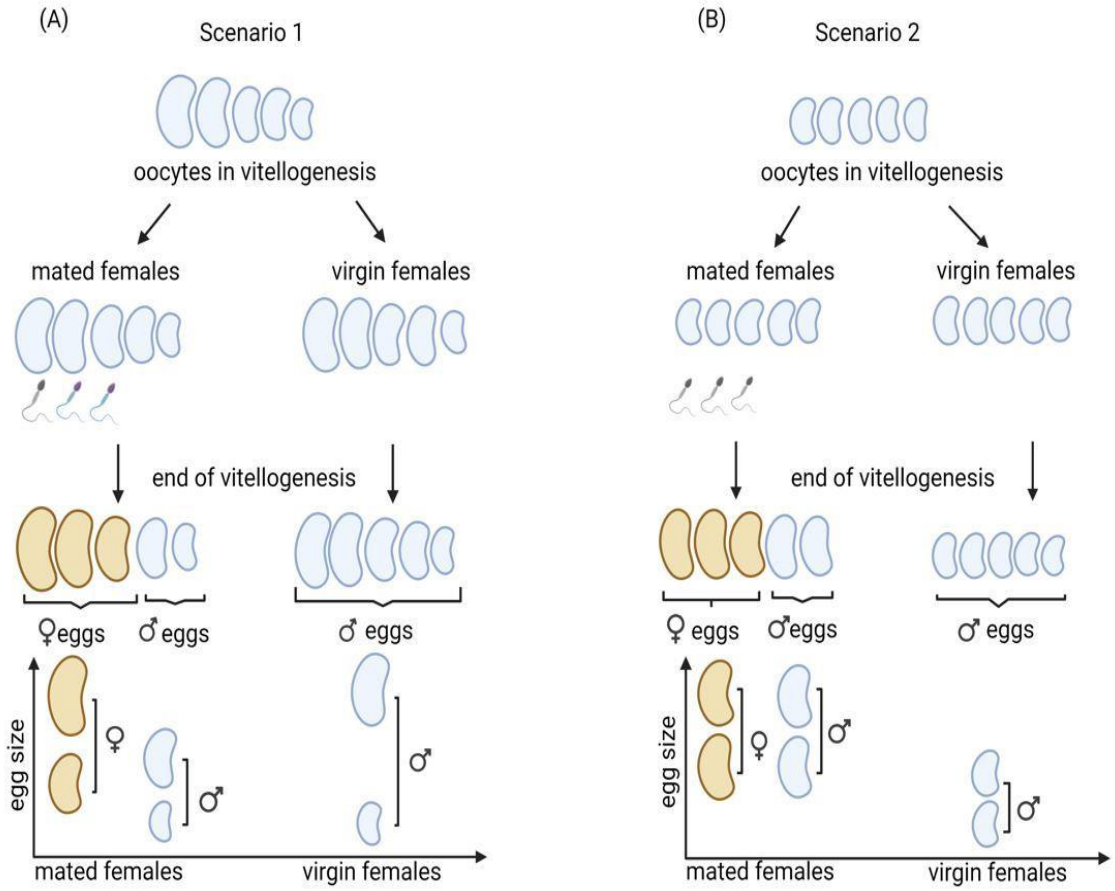


Figure 5. Hypothetical mechanisms of sex-specific egg size in haplodiploid arrhenotokous lineages of *T. tabaci*. (A) Scenario 1: Differences in egg size exist before fertilization, and egg size determines the probability of an egg being fertilized. Under this scenario, the egg size range between virgin and mated mothers should be the same. (B) Scenario 2: Egg size is equal in virgin and mated mothers prior to fertilization, and mating increases egg size in general. Straight vertical lines represent egg size ranges. Fertilized and unfertilized eggs are presented in brown and blue, respectively (MUSA et al. 2022).

3.9.3. Comparison of male egg size produced by virgin and mated mothers of the L1 and T lineages

Using only male eggs, we compared the size of the eggs (width, length, and volume) of males produced by virgin and mated mothers for the entire lifespan of the mothers and in the above-mentioned age groups. For this analysis a one-way multivariate analysis of variance MANOVA was run, with the factor of 'mating status'.

3.10. Effect of maternal age on the egg size

To investigate the effect of maternal age on egg size independently of the offspring sex, we used eggs produced by mated and virgin mothers of the L1, L2 and T lineages. The age of the ovipositing mothers was recorded for each egg they laid until the mothers died. In the case of the L1 and T lineages, egg volumes were modelled depending on the maternal age for their entire lifespan and age groups: 3–5 days, 7–10 days and above 10 days. In the case of the L2 lineages, egg volume was modelled throughout the maternal age, 1-10 days old and above 10 days old. The maternal age effect on egg size in males and females of the L1, L2 and T lineages was analysed with linear regression models. The slopes of the trends were calculated and tested to see if they were significant.

3.11. Morphometric analysis of the *T. tabaci* species complex

3.11.1. Morphometric analysis of the eggs

Morphometric analyses of the eggs were performed to obtain information on the morphological variations among the three lineages of *T. tabaci*. The size of the eggs was compared between L1, L2 and T lineages using a three-way block design MANOVA with the factors 'lineages, mated status, gender and block mother. Eggs of the L2 lineage were compared with all other eggs with a two-sample independent Student's t-test and corrected by Welch.

3.11.2. Morphometric analysis of first instar larvae and adults

Principal Component Analysis (PCA) was used to find traits responsible for the variation amongst first instar larvae and adults of the three lineages. Variables D3 pronotumand D7 pronotum were transformed by Box-Cox transformation of lambda=-2 (i.e. trD3 pronotum =-(1/D3 pronotum) 2 and trD7 pronotum =-(1/D7 pronotum) 2. Because of serious multicollinearity, D3 metanotum, D2 tergite II, D4 head and (transformed) D7 pronotum were eliminated from the analysis of larvae as they were highly significantly correlated with other variables (Table 5). Because of the same reason, the variables S3 tergite IV and Discal.s.3 were eliminated from the analysis of adults (Table 5). In this way, we could ensure that PCA requirements (i.e., normally distributed variables having no multicollinearity among them) were satisfied.

Table 5. The most significant correlation coefficients (all at ***p<0.001) were calculated pairwisely among larval and adult characters. The characters in bold were kept in the analysis and all others were eliminated.

Parameters (Larvae)		Pearson's correlation coefficient	Parameters (Adults)		Pearson's correlation coefficient
D3 metanotum	**D4 metanotum**	0.96***	S3 terg.IV	Discal.s.3	0.99***
D4 metanotum	D2 terg.II	0.91***	**Meta.s.1**	Discal.s.3	0.97***
D2terg.II	**D2 terg.VIII**	0.90***	**Meta.s.1**	S3 terg.IV	0.96***
D3 metanotum	D2terg.II	0.89***	**P.a.s**	S3 terg.IV	0.93***
D4 metanotum	**D2 terg.VIII**	0.87***	**S2 terg.VIII**	Discal.s.3	0.93***
D3 head	D4 head	0.86***	**P.a.s**	Discal.s.3	0.92***
D3 metanotum	**D2 terg.VIII**	0.86***	S3 terg.IV	**S2 terg.VIII**	0.91***
D7 pronotum†	**D3 pronotum†**	0.86***	**Oc.s.2**	Discal.s.3	0.89***

Note: † Transformed variable with Box-Cox lambda=-2.

3.12. Statistical analysis

The statistical analyses were performed using IBM SPSS (v. 25) and R (v.4.1.2). The normality of the residuals was accepted by the absolute values of their skewness and kurtosis, as they were all below 1. The homogeneity of variance was tested with Levene's test ($p > 0.05$). In the case of the comparison between male and female egg size produced by mated mothers, the comparison of egg size between virgin and mated mothers, and the comparison of male egg size produced by virgin and mated mothers, when there was a significant overall MANOVA result, one-way between-subject effects were tested for all three variables (width, length, and volume) with Bonferroni's adjustment. In the case of the comparisons between egg size of the L1, L2, and T lineages and when there was a significant overall MANOVA result, robust three-way between-subject effects were tested for all three variables (width, length, and volume) with Bonferroni's adjustment since inhomogeneity of variance was detected by Levene's test ($p<0.05$).

4. RESULTS AND DISCUSSION

4.1. *Thrips tabaci* lineage identification

Based on the analysis of the mtCOI region, 87 mated and virgin females of the L1, L2, and T lineages and 36 males of both the L1 and T lineages, which were mated with their conspecific females (whose progeny were used in this study), proved to belong to the lineage as expected.

4.2. Effect of mating and egg size on the hatching probability of the eggs

Maternal mating status significantly influenced the probability of hatching in the L1 lineage. The overall number of oviposited eggs was 1305; 67% of 598 eggs and 44% of 707 eggs laid by virgin and mated mothers, respectively, hatched. Therefore, virgin mothers had a significantly higher probability of having eggs that hatched, whereas mated mothers had a significantly higher probability of having eggs that did not hatch ($X^2 = 68.962$, df = 1, $p < 0.001$). In the T lineage, the overall number of oviposited eggs was 2660; 61% of 1558 and 58% of 1102 eggs laid by virgin and mated mothers, respectively, hatched. Mating status did not influence the probability of hatching ($X2 = 2.098$, df = 1, $p = 0.147$). Moreover, egg size did not influence the probability of hatching in the virgin mothers of the L1 lineage (Wilk's $\lambda = 0.99$, $F(3:569) = 1.585$, $p = 0.19$; see Table 6), whereas in the mated mothers of the L1 lineage, eggs that hatched were significantly larger than eggs that did not hatch (Wilk's $\lambda = 0.98$, $F(3:688) = 3.712$, $p < 0.05$; see Table 6). For both virgin and mated mothers of the T lineage, egg size significantly influenced the probability of hatching. Eggs that hatched were significantly larger than eggs that did not hatch (Virgin: Wilk's $\lambda = 0.98$, $F(3:1529) = 9.19$, $p < 0.001$; Mated: Wilk's $\lambda = 0.98$, $F(3:1080) = 7.083$, $p < 0.001$; see Table 6). The significant differences were all manifested in the width and volume but not in the length of the eggs (width and volume, L1 mated: $F(1:690) > 7.534$, $p < 0.05$; T virgin: $F(1:1531) > 12.716$, $p < 0.01$; T mated: $F(1:1082) > 6.710$, $p < 0.05$; length, L1 mated: $F(1:690) = 0.011$, $p = 0.92$; T virgin: $F(1:1531) = 5.171$, $p = 0.07$; T mated: $F(1:1082) = 0.977$, $p = 0.32$).

Table 6. Size of hatched and unhatched eggs in the virgin and mated mothers of the L1 and T lineages.

Lineage	Mother status	Hatchability	N	Width (µm)	Length (µm)	Volume (µm)^3
L1	Virgin	Hatched (67%)	398	101.63±5.23a	210.79±7.53a	1143028±122622a
		Did not hatch	200	100.14±5.49a	210.79±8.54a	1110542±131482a
	Mated	Hatched (44%)	308	104.69±4.56b	215.82±7.54a	1241697±124026b
		Did not hatch	399	103.92±4.88a	214.99±8.55a	1218441±123413a
T	Virgin	Hatched (61%)	947	97.15±3.77b	196.19±7.55a	971065±86207b
		Did not hatch	611	96.39±4.48a	195.38±8.52a	953078±102088a
	Mated	Hatched (58%)	639	96.25±3.64b	197.11±7.74a	957504±81936b
		Did not hatch	463	95.48±4.99a	196.90±7.74a	942762±106616a

Data are presented as mean ± SD. N: number of tested individuals. Different letters indicate significant differences in egg size ($p<0.05$).

Egg size is considered a reliable indicator of maternal investment in offspring fitness (FOX and CZESAK 2000). The relationship between egg size and hatchability has already been studied for mites (MACKE et al. 2011b), but never for thrips. The fact that larger eggs are generally more likely to hatch and produce fast-developing juveniles with higher survivorship than smaller eggs in the spider mite *T. urticae* indicates that egg size might be a predictor of energy content in some cases (MACKE et al. 2011b), and our results confirm this: hatched eggs were significantly larger than the eggs that did not hatch in the L1 lineage laid by mated mothers and in the T lineage of *T. tabaci* for all eggs, independently of mating status. Mating also affected the hatching probability of the eggs in the L1 lineage, with more eggs hatching from virgins than from mated mothers, and mating did not affect the hatching probability of the eggs in the T lineage. Mating (once or multiple times) had no discernible effect on the hatchability of eggs in the bruchid beetle *Callosobruchus maculatus* (Fabricius) (FOX 1993). To our knowledge, no other study has tested the effect of mating status on the hatching probability of eggs in arthropods.

4.3. Egg size and sex allocation

4.3.1. Comparison of male and female egg size produced by mated mothers of the L1 and T lineages

Considering all the eggs measured throughout the entire lifespan of the mothers, there were no significant differences in the size of male and female eggs produced by mated mothers in either the L1 or T lineages (L1 lineage: Wilk's $\lambda = 0.97$; $F(3:202) = 2.291$, $p = 0.08$; T lineage: Wilk's $\lambda =$

0.98; F (3:428) = 2.528, p = 0.06; see Table 7). The mean lifespan of mated mothers in the L1 lineage was 14.59 days with a standard deviation of 4.73, whereas, for the mated mothers of the T lineage, the mean lifespan was 20.66 days with a standard deviation of 6.96.

Table 7. Size of male and female eggs produced by mated mothers of the L1 and T lineages throughout the lifespan.

	Gender	N	Width (µm)	Length (µm)	Volume $(\mu m)^3$
L1	Male	91	103.68 ± 4.92	215.33 ± 8.24	1215783 ± 133761
	Female	119	105.00 ± 4.31	215.25 ± 7.49	1245540 ± 120556
T	Male	112	95.80 ± 3.60	196.50 ± 8.11	946061 ± 85649
	Female	325	96.61 ± 3.47	197.54 ± 7.77	966454 ± 77236

Data are presented as mean ± SD. N: number of tested individuals.

There were no significant differences in the size of male and female eggs produced by mated mothers of the L1 lineage at any given age group, either: (3-5 day old mothers: Wilk's $\lambda = 0.95$; F (3: 48) = 0.838, p = 0.48; 7-10 day old mothers: Wilk's $\lambda = 0.98$; F (3:60) = 0.441, p = 0.73; above 10-day old mothers: Wilk's $\lambda = 0.94$; F (3:44) = 0.916, p = 0.44; Table 8).

In the T lineage, the size of male and female eggs produced by mated mothers was not significantly different at the age group 3-5 day old mothers and above 10-day old mothers (3-5 day old mothers: Wilk's $\lambda = 0.92$; F (3:63) = 1.945, p = 0.13; above 10-day old mothers: Wilk's $\lambda = 0.96$; F (3:192) = 2.459, p = 0.06), while the difference was significant at the age group of 7-10 days (Wilk's $\lambda = 0.90$; F (3:104) = 3.978, $p < 0.05$; Table 8). According to the follow-up univariate analysis, at this age, only the width of female eggs was significantly larger than that of male eggs (Table 8).

Table 8. Size of male and female eggs produced by mated mothers of L1 and T lineages at different age groups.

Lineage	Age	Gender	N	Width (µm)	Length (µm)	Volume (µm)^3
L1	3-5	Male	32	105.39±4.50	215.00±6.19	1252784±115861
		Female	20	105.75±4.81	214.63±8.24	1261308±145849
	7-10	Male	20	104.50±4.56	218.75±8.29	1253601±126684
		Female	44	105.51±4.09	217.90±7.55	1272476±113299
	>10	Male	18	101.94±5.66	211.25±7.63	1153668±141059
		Female	30	103.50±4.08	211.75±6.40	1189676±101846
T	3-5	Male	20	97.38±4.01	199.00±7.23	989357±85396
		Female	47	96.38±2.75	199.31±7.78	969857±60965
	7-10	Male	17	95.15±3.59	198.53±8.34	943690±94740
		Female	91	97.69±3.19*	195.82±7.67	979679±75671
	>10	Male	50	95.20±3.60	194.30±8.69	923248±81207
		Female	146	95.92±3.69	197.53±7.76	953196±83045

Data are presented as mean ± SD. N: number of tested individuals. * is for significant gender differences in the width of the eggs ($p < 0.05$).

Our key finding is that sex allocation in haplodiploid *T. tabaci* is not mediated via egg size like in the two-spotted spider mite *T. urticae* (MACKE et al. 2011b) and in Kelly's citrus thrips *P. kellyanus* (KATLAV et al. 2020). In both species, egg size and gender were found to be related with egg mass that was produced by young arrhenotokous females, 3-5 day old mothers in *T. urticae* and 7-10 day old mothers in *P. kellyanus*. The size of male and female eggs produced by mated mothers of the L1 lineage was not significantly different for the whole lifespan and at any age group, indicating that gender and egg size are independent of each other in this lineage regardless of maternal age. In the T lineage, gender seemed to be dependent on egg size, however, only in the maternal age group of 7-10 days, but gender was independent of egg size in the progeny of younger and older mothers. Our results demonstrate that studying the relationship between egg size and gender in a narrow age group of mothers might lead to misconclusions, unless there are different mechanisms working in mated females depending on their age.

4.3.2. Testing the model of egg size and sex allocation

From all the eggs measured throughout the lifespan of the virgin and mated mothers of the L1 and T lineages, our results show that eggs laid by mated mothers were significantly larger than eggs laid by virgin mothers in the L1 lineage (Wilk's $\lambda = 0.86$, $F(3:1301) = 72.523$, $p < 0.001$; Table 9).

That was true for all three parameters of the egg size ($F(3:1303) > 105.092$, $p<0.001$). In the T lineage, eggs laid by virgin mothers were significantly larger (Wilk's $\lambda = 0.98$, $F(3:2656) = 16.624$, $p < 0.001$; Table 9) in width and volume compared to the eggs laid by mated mothers for the entire lifespan ($F(3:2658) > 11.980$, $p<0.01$), though with a significantly smaller length ($F(3:2658) = 13.980$, $p < 0.001$).

Table 9. Size of eggs produced by virgin and mated mothers of the L1 and T lineages throughout the lifespan.

Lineage	Mating status	N	Width (µm)	Length (µm)	Volume $(\mu m)^3$
L1	Virgin	598	101.13±3.16a	210.79±7.87a	1132163±126478a
	Mated	707	104.26±4.75b	215.35±8.13b	1228572±124131b
T	Virgin	1558	96.85±4.08b	195.87±7.95a	964011±93143b
	Mated	1102	95.92±4.27a	197.02±7.74b	951310±93344a

Data are presented as mean ± SD. N: number of tested individuals. Different letters indicate significant differences in egg size ($p < 0.05$).

In the L1 lineage, eggs laid by mated mothers were significantly larger than eggs laid by virgin mothers at all maternal age groups: (3-5 day old mothers: Wilk's $\lambda = 0.80$, $F(3:312) = 25.958$, $p < 0.001$; 7-10 day old mothers: Wilk's $\lambda = 0.81$, $F(3:328) = 26.403$, $p < 0.001$; and above 10 day old mothers: Wilk's $\lambda = 0.95$, $F(3:420) = 7.654$, $p < 0.001$; Table 10). That was true for all three parameters of egg size ($F(1:df) > 8.5$, df = 314, 330 and 422, respectively, $p < 0.01$), except for the width of eggs laid by mothers older than 10 days, at which the difference in the size of eggs between virgin and mated mothers was not significant ($F(1:422) = 1.873$, $p = 0.172$).

In the T lineage, eggs laid by mated mothers were significantly larger than eggs laid by virgin mothers in the maternal age group of 3-5 day old mothers (Wilk's $\lambda = 0.96$, $F(3:388) = 5.926$, $p < 0.01$; Table 10), which were detected in the width, length, and volume of the eggs ($F(1:390) > 8.511$, $p < 0.01$). Meanwhile, at the maternal age of 7-10 day old mothers, there was no significant difference in the size of eggs laid by virgin and mated mothers (Wilk's $\lambda = 0.99$, $F(3:555) = 2.315$, $p=0.075$; Table 10), even though eggs produced by virgin mothers were slightly larger in width and volume than those produced by mated mothers. The difference was significant above 10 days of maternal age (Wilk's $\lambda = 0.96$, $F(3:1389) = 21.093$, $p < 0.001$; Table 10): eggs produced by virgin mothers were significantly larger than eggs produced by mated mothers for the

width and egg volume, while eggs produced by mated mothers were significantly larger than those produced by virgin mothers, considering the length of the egg ($F(1:1391) > 10.329$, $p < 0.01$).

Table 10. Size of eggs produced by virgin and mated mothers of the L1 and T lineages at different age groups.

Lineage	Age	Mating status	N	Width (µm)	Length (µm)	Volume $(\mu m)^3$
L1	3-5	Virgin	154	100.50±5.31a	211.85±7.89a	1124142±128114a
		Mated	162	105.05±4.29b	215.15±7.95b	1245716±117415b
	7-10	Virgin	114	102.48±4.73a	210.50±8.35a	1159649±114080a
		Mated	218	105.02±4.42b	216.95±7.81b	1254857±111360b
	>10	Virgin	222	101.80±4.72a	210.38±7.42a	1144270±115555a
		Mated	202	102.45±5.04a	213.68±8.03b	1177647±127352b
T	3-5	Virgin	220	95.33±4.28a	196.91±7.55a	939622±99414a
		Mated	172	96.60±3.89b	199.16±7.59b	974596±85654b
	7-10	Virgin	342	97.57±3.98a	197.22±7.13a	984918±88818a
		Mated	217	96.83±3.73a	196.46±7.54a	966120±83611a
	>10	Virgin	836	97.14±3.89b	194.91±8.28a	964865±90767b
		Mated	557	95.60±4.41a	196.33±7.76b	941784±96684a

Data are presented as mean ± SD. N: number of tested individuals. Different letters indicate significant differences in egg size ($p < 0.05$).

To summarize our results, we can state that the size distribution of the eggs of virgin and mated mothers compared within the L1 and the T lineages are all normal with homogeneous variances, whether considering the entire lifespan of the mothers or the different age groups of the mothers. The only difference we found was in the mean values of the egg size distribution. Specifically, for the L1 lineage, the eggs of mated mothers are significantly larger (independently of which age group of the mothers is considered). In the T lineage, it seems that in the younger age group, the eggs of mated mothers are marginally larger but the opposite is observed in the older age group, where the eggs of virgin mothers are marginally larger.

By comparing the size of eggs produced by virgin and mated mothers, we showed that mated females laid significantly larger eggs throughout their lifespan and in all other age groups in the L1 lineage. The mean value of the egg size distribution of mated mothers in the L1 lineage was larger than that of virgins throughout their lifespan. This may suggest that there is no egg size that determines fertilization in this lineage, but rather it is the fertilization that may influence egg size.

Eggs produced by mated mothers might receive more resources than those produced by virgins, and mating just increases egg size in general; leading to a larger size of male eggs produced by mated mothers than by virgins (Figure 2B, scenario 2). Contrary to the L1 lineage, in the T lineage, an entirely new scenario is needed to assess the obtained results; eggs laid throughout the lifespan of virgin mothers were marginally larger than those of mated mothers.

Our findings may indicate that these two lineages of *T. tabaci* have different resource allocation strategies in response to maternal mating status. In *P. kellyanus* (KATLAV et al. 2020), mating increases the early-life reproductive investment of females; therefore, mated females produce larger eggs than virgin females, just like our L1 lineage. However, male offspring of mated mothers had smaller eggs than those of virgins (KATLAV et al. 2020). In *Tetranychus ludeni* Zacher, virgin mothers laid significantly larger eggs than mated mothers, indicating a strategic resource allocation in response to mating status, with more resources being allocated to their male offspring when the mothers do not have the chance to produce female offspring (ZHOU et al. 2018). Because males may provide nutrients to females with their ejaculation, mating is an activity of females that manipulates their nutritional status and therefore influences the size of their eggs. These nuptial gifts serve as paternal investment by increasing reproductive fitness (e.g., increasing egg size; GWYNNE 1984). Multiple mating of a female bruchid beetle *C. maculatus* F. has been shown to increase the size of eggs laid by her (FOX 1993). In haplodiploids, males can only pass their genes to female offspring, whereas the genes of females are passed on to both males and females. The effort of males to influence female production results in sexual conflict between males and females over the sex ratio of the progeny. During mating, males may transfer some seminal proteins that increase the sperm release from the spermatheca, which facilitates the fertilization rate (SHUKER et al. 2009). A higher fertilization rate could also be achieved by increasing egg size after mating (MACKE et al. 2012). Moreover, if the selection of females has optimized egg size, females will use male nutrients to increase egg numbers. In contrast, male selection would favour increasing the size of the eggs he fertilizes rather than increasing the number of eggs (WICKLER 1985). This change in the egg size could be manipulated by shifting adaptations between early and late reproduction or between size and the number of offspring (EBERHARD 1996). Further studies into sexual conflicts and sex allocation patterns need to be carried out in order to better understand the observed phenomenon in this cryptic species complex.

4.3.3. Comparisons of male egg size produced by virgin and mated mothers of the L1 and T lineages

The size of male eggs produced by mated mothers was significantly larger than that produced by virgin mothers for the whole lifespan in the L1 lineage (Wilk's $\lambda = 0.93$, $F(3:680) = 18.261$, $p < 0.001$; Table 11). Highly significant differences were detected in all three parameters of the eggs: the width, length, and volume ($F(1:682) > 22.200$, $p < 0.001$). In the T lineage, there were no significant differences in the size of male eggs produced by virgin or mated mothers throughout the lifespan (Wilk's $\lambda = 0.99$, $F(3:1657) = 2.097$, $p = 0.10$; Table 11).

Table 11. Size of male eggs produced by virgin and mated mothers of the L1 and T lineages throughout the lifespan.

Lineage	Male produced by	N	Width (µm)	Length (µm)	Volume $(\mu m)^3$
L1	Virgin mother	597	101.21 ± 5.23a	210.80 ± 7.87a	1133672 ± 124205a
	Mated mother	91	103.68 ± 4.92b	215.33 ± 8.24b	1215783 ± 133761b
T	Virgin mother	1555	96.85 ± 4.06	195.90 ± 7.82	964029 ± 91621
	Mated mother	111	95.77 ± 3.60	196.82 ± 7.36	947036 ± 85410

Data are presented as mean ± SD. N: number of tested individuals. Different letters indicate significant differences in egg size ($p < 0.05$).

In the L1 lineage, the size of male eggs produced by mated mothers was significantly larger than that produced by virgin mothers at the maternal age groups of 3-5 day old and 7-10 day old mothers (Wilk's $\lambda = 0.84$, $F(3:182) = 11.576$, $p < 0.001$; Wilk's $\lambda = 0.86$, $F(3:130) = 7.298$, $p < 0.001$, respectively; Table 12). At maternal age above 10 days old, there were no significant differences in the size of male eggs produced by virgin and mated mothers (Wilk's $\lambda = 0.99$, $F(3:236) = 0.596$, $p=0.62$; Table 12).

In the T lineage, there were no significant differences in the size of male eggs produced by virgin and mated mothers at the maternal age groups of 3-5 day old and 7-10 day old mothers (Wilk's $\lambda = 0.98$, $F(3:236) = 1.624$, $p=0.19$; Wilk's $\lambda = 0.98$, $F(3:355) = 2.423$, $p=0.07$; Table 12). Moreover, at maternal age above 10 days old, there were significant differences in male egg size produced by virgin and mated mothers (Wilk's $\lambda = 0.99$, $F(3:882) = 3.966$, $p < 0.01$; Table 12); eggs produced by virgin mothers were significantly larger than eggs produced by mated mothers, considering both the width and volume of the eggs.

Table 12. Size of male eggs produced by virgin and mated mothers of the L1 and T lineages at different age groups.

Lineage	Age	Male produced by	N	Width(µm)	Length (µm)	Volume (µm)^3
L1	3-5	Virgin mother	154	100.50±5.31a	211.85±7.89a	1124142±128114a
		Mated mother	32	105.39±4.50b	215.00±6.19b	1252784±115861b
	7-10	Virgin mother	114	102.48±4.73a	210.50±8.35a	1159649±114080a
		Mated mother	20	104.50±4.56b	218.75±8.29b	1253601±126684b
	>10	Virgin mother	222	101.80±4.72a	210.38±7.42a	1144270±115555a
		Mated mother	18	101.94±5.66a	211.25±7.63a	1153668±141059a
T	3-5	Virgin mother	220	95.33±4.28a	196.91±7.55a	939622±99414a
		Mated mother	20	97.38±4.01a	199.00±7.23a	989357±85396a
	7-10	Virgin mother	342	97.57±3.98a	197.22±7.13a	984918±88818a
		Mated mother	17	95.15±3.59a	198.53±8.34a	943690±94740a
	>10	Virgin mother	836	97.14±3.89b	194.91±8.28a	964865±90767b
		Mated mother	50	95.20±3.60a	194.30±8.69a	923248±81207a

Data are presented as mean ± SD. N: number of tested individuals. Different letters indicate significant differences in egg size ($p < 0.05$).

4.4. Effect of maternal age on the egg size

Egg volumes depending on maternal age are presented for the whole lifespan of the mated and virgin mothers of L1 and T lineages in Figure 6. The trend of male egg volumes produced by mated mothers in the L1 lineage is slightly significantly decreasing with slope s = -6306 ($p = 0.06$) (Figure 6A). For the L1 lineage, the trend of female egg volumes produced by mated mothers is also significantly decreasing with slope s = -7522 ($p < 0.01$, Figure 6B). In Figures 6C and 6D, the male and female egg volumes produced by mated mothers of the T lineage are presented, for which the trends are significantly decreasing (s = -2866, $p < 0.01$; s =-2087, $p < 0.01$, respectively). For the L1 lineage, the trend of male egg volumes produced by virgin mothers is significantly increasing with slope s = 3223 ($p<0.01$, Figure 6E). In the case of the T lineage, the trend of male egg volume produced by virgin mothers is not significant with the slope s = 501 ($p = 0.204$, Figure 6F).

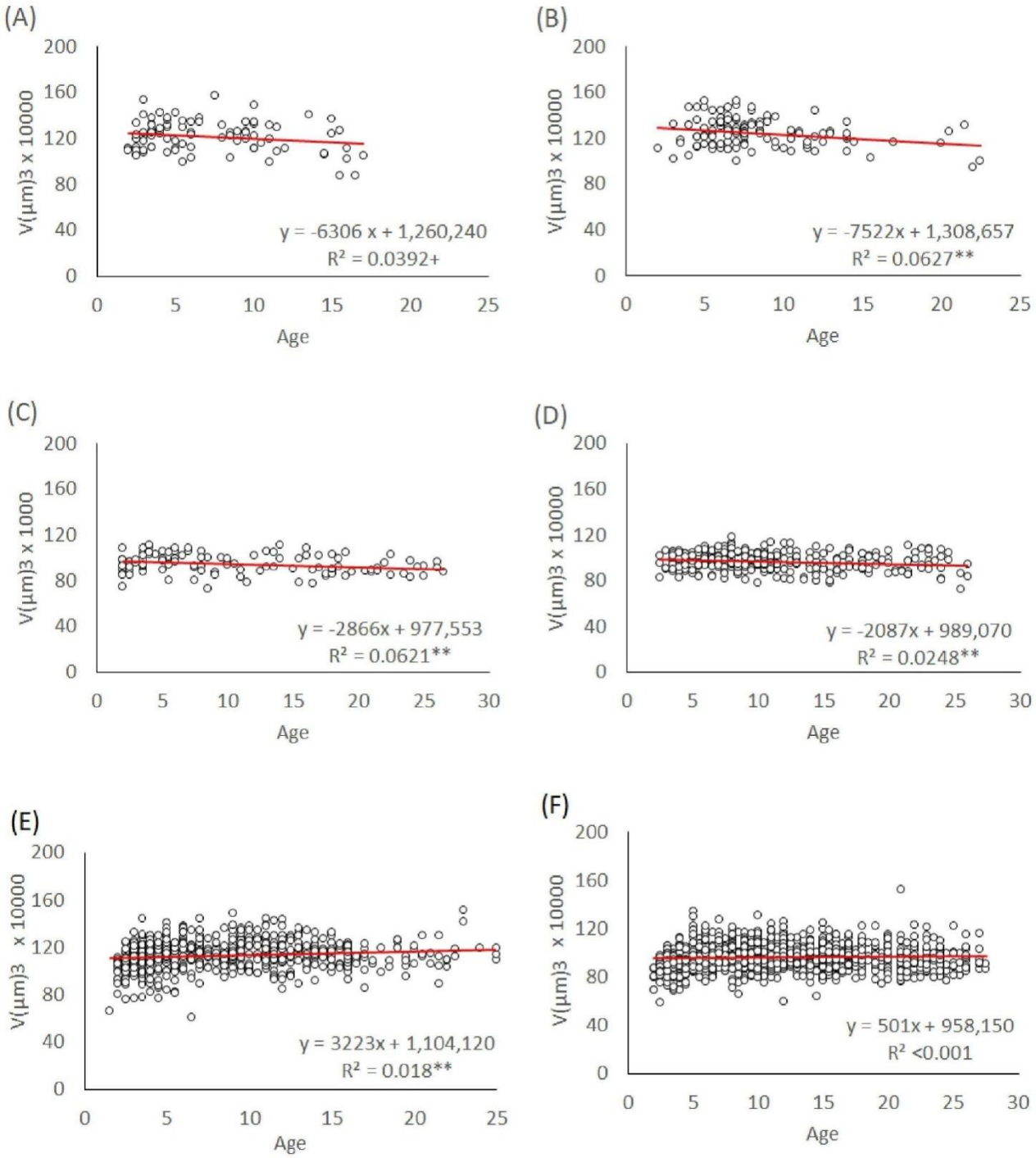


Figure 6. Linear regression of egg size throughout the lifespan of mated and virgin mothers of the L1 and T lineages. (A) L1 male eggs of mated mothers, (B) L1 female eggs of mated mothers, **(C)** T male eggs of mated mothers, (D) T female eggs of mated mothers, (E) L1 male eggs of virgin mothers, (F) T male eggs of virgin mothers.

The significance level of the slope: **$p < 0.01$; +$p < 0.1$

Egg volumes in maternal age of 3-5 day old mated and virgin mothers of the L1 and T lineages are shown in Figure 7. In the case of the L1 lineage, the trends of male and female egg volumes produced by mated mothers are not significant ($s = -34434$, $p = 0.91$; $s = 66527$, $p = 0.20$, respectively; Figures 7A, 7B). In Figures, 7C and 7D, the male and female egg volumes of mated mothers of the T lineage are represented, for which the trends are not significant either ($s = 14635$, $p = 0.56$; $s = -8311$, $p = 0.55$, respectively). In the case of the L1 and T lineages, the trends of male egg volumes produced by virgin mothers are significantly increasing ($s = 27398$, $p = 0.06$; $s = 32816$, $p < 0.001$, respectively; Figures 7E, 7F).

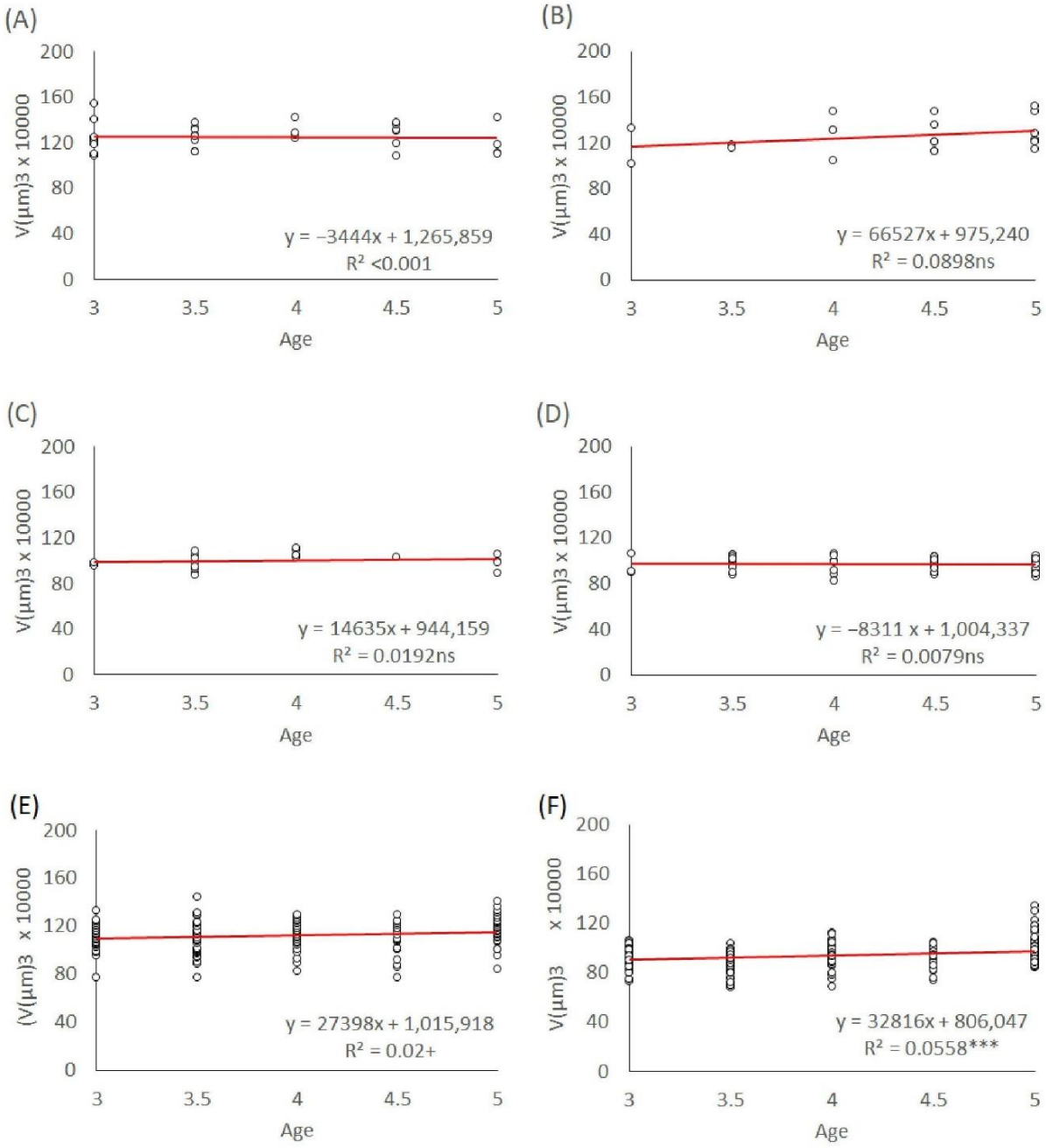


Figure 7. Linear regression of egg size in the maternal age group of 3-5 day old mated and virgin mothers of the L1 and T lineages (A) L1 male eggs of mated mothers, (B) L1 female eggs of mated mothers, (C) T male eggs of mated mothers, (D) T female eggs of mated mothers, (E) L1 male eggs of virgin mothers, (F) T male eggs of virgin mothers.

The significance level of the slope: ns not significant; +$p < 0.1$; ***$p < 0.01$

Egg volumes in maternal age of 7-10 day old mated and virgin mothers of the L1 and T lineages are shown in Figure 8. For both the L1 and T lineages, the trends of male and female egg

volumes produced by mated mothers are not significant (s = -32058, p = 0.40; s = -64123, p = 0.76; s = -10863, p = 0.66; s = -129267, p = 0.10, respectively; Figures 8A, 8B, 8C, 8D). For the L1 and T lineages, the trends of male egg volumes of virgin mothers are also not significant (s = 5230, p = 0.618; s = -4626, p = 0.287, respectively; Figures 8E and 8F).

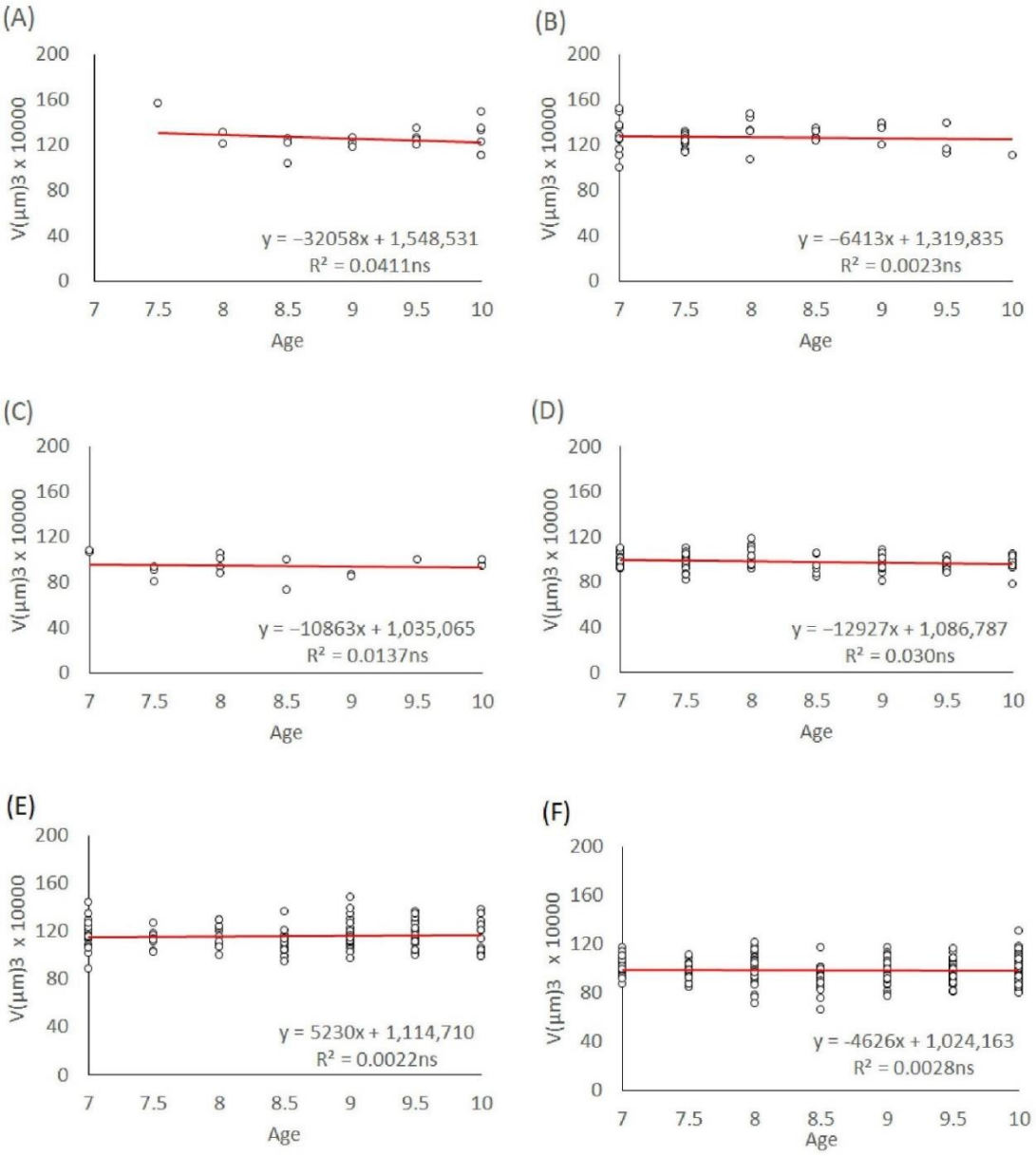


Figure 8. Linear regression of egg size in the maternal age group of 7-10 day old mated and virgin mothers of the L1 and T lineages. (A) L1 male eggs of mated mothers, (B) L1 female eggs of mated mothers, (C) T male eggs of mated mothers, (D) T female eggs of mated mothers, (E) L1 male eggs of virgin mothers, (F) T male eggs of virgin mothers.

The significance level of the slope: ns not significant

For maternal age groups above 10 days, egg volumes of mated and virgin mothers of the L1 and T lineages are shown in Figure 9. The trends of male and female egg volumes produced by mated mothers are not significant in either of the L1 and T lineages ($s = -21463$, $p = 0.21$; $s = -8404$, $p = 0.100$; $s = -2699$, $p = 0.30$; $s = -1547$, $p = 0.30$, respectively; Figures 9A, 9B, 9C, 9D). In the case of the L1 lineage, the trend of male egg volume produced by virgin mothers is also not significant, with a slope of $s = -1733$ ($p = 0.441$, Figure 9E). For the T lineage, the trend of male egg volume in virgin mothers is slightly significantly decreasing with the slope $s = -1441$ ($p = 0.05$, Figure 9F).

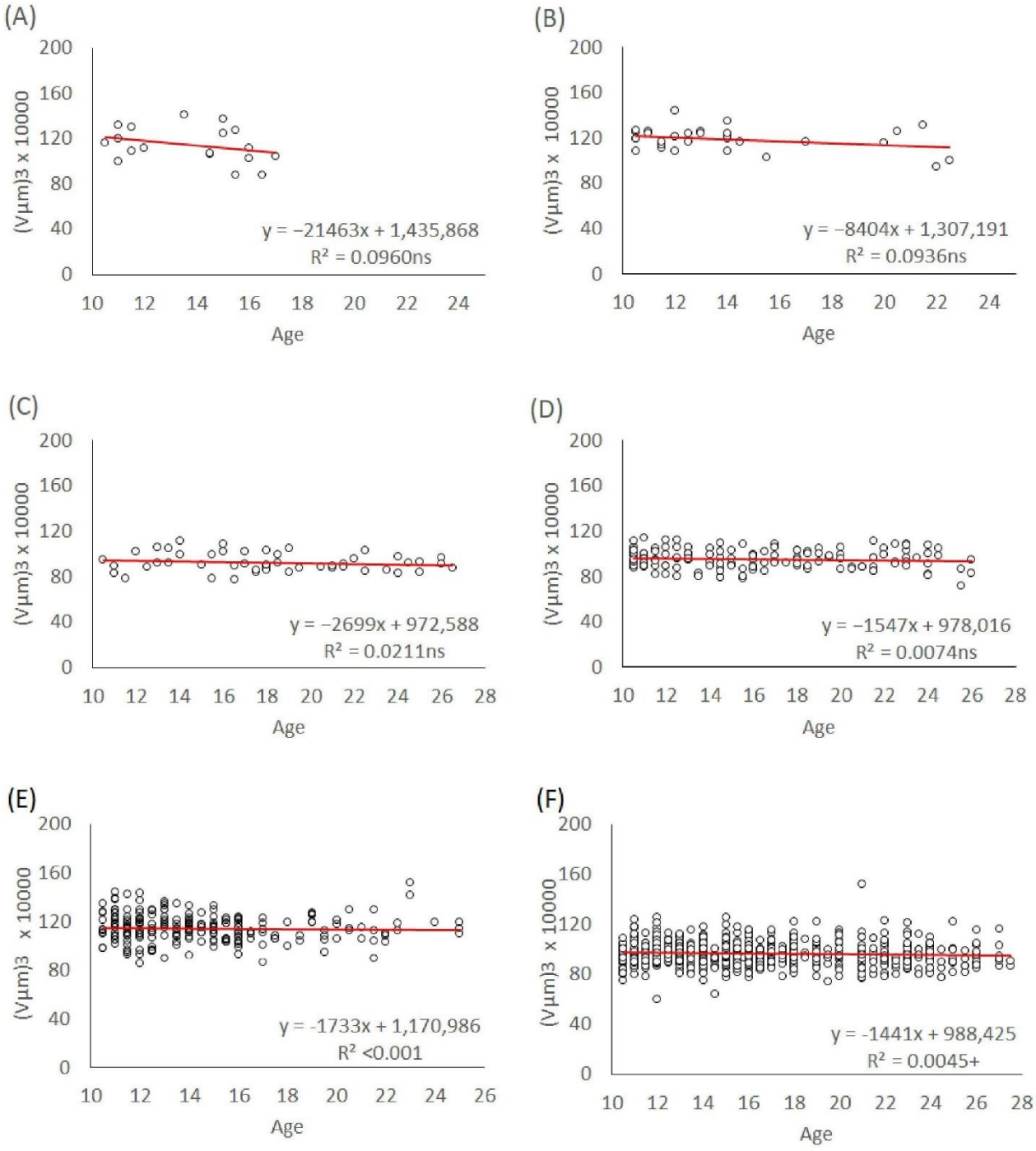


Figure 9. Linear regression of egg size in the maternal age group above 10 days old mated and virgin mothers of the L1 and T lineages. (A) L1 male eggs of mated mothers, (B) L1 female eggs of mated mothers, (C) T male eggs of mated mothers, (D) T female eggs of mated mothers, (E) L1 male eggs of virgin mothers, (F) T male eggs of virgin mothers.

The significance level of the slope: ns is not significant; +$p < 0.1$

Egg volume depending on the maternal age of the L2 lineage is presented in Fig. 10. The trends of the female eggs throughout the lifespan of the mothers, 1-10 days old and above 10 days old are all significantly increasing ($s = 6603.41$, $p<0.001$; $s = 12046.9$, $p<0.001$; $s = 7892.12$, $p<0.05$; respectively: Figure 10A, 10B, 10C).

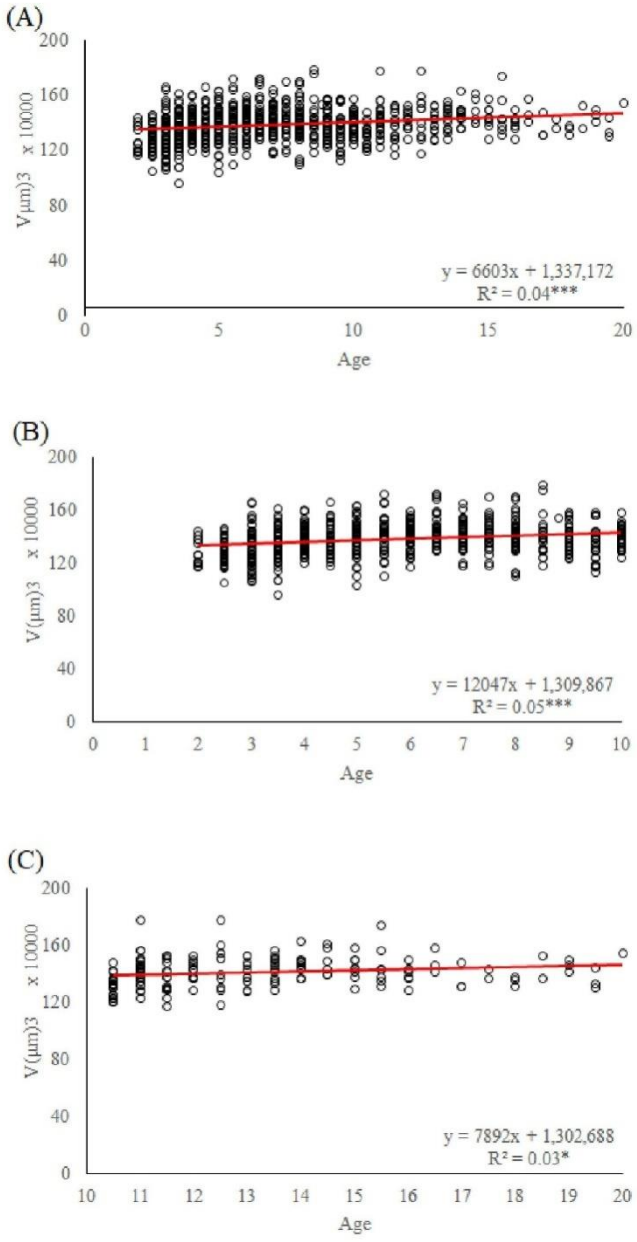


Figure 10. Liner regression of egg size in different age groups of the mothers in the L2 lineage. (A) throughout the lifespan, (B) 1-10 days old, (C) above 10 days old.

The significance level of the slope: ***p < 0.001; +p < 0.1

The range of slopes goes from 40671.04 to 6603.41 (Figure 11). Although they are all positive and significant, the slopes are decreasing linearly. And the slopes calculated from day 11 and further, up to day 20 (i.e., 11-20, 12-20, 13-20, etc.) are around a constant (~8000), ranging from 9126.77 to 6603.41. The linearly decreasing slope pattern up to day 10 and the nearly constant pattern of it later are very well-separated (i.e., the change from a linear decrease to almost no change is sudden). The slopes of linear trends of egg sizes depending on the mother's age, starting from a moving point day 5 or later to a fixed end point day 20, are increasing to day 9, but the slopes are significant only in 5 cases (2-8; 2-8.5; 2-9; 2-9.5; 2-10) coloured in red; these significant results, however, can be caused by some low egg sizes. So, we ought not to evaluate these trends as significant. Day 10 as a cut point, however, does exist but after this age, the positive linear trend does not change notably as it did before day 10.

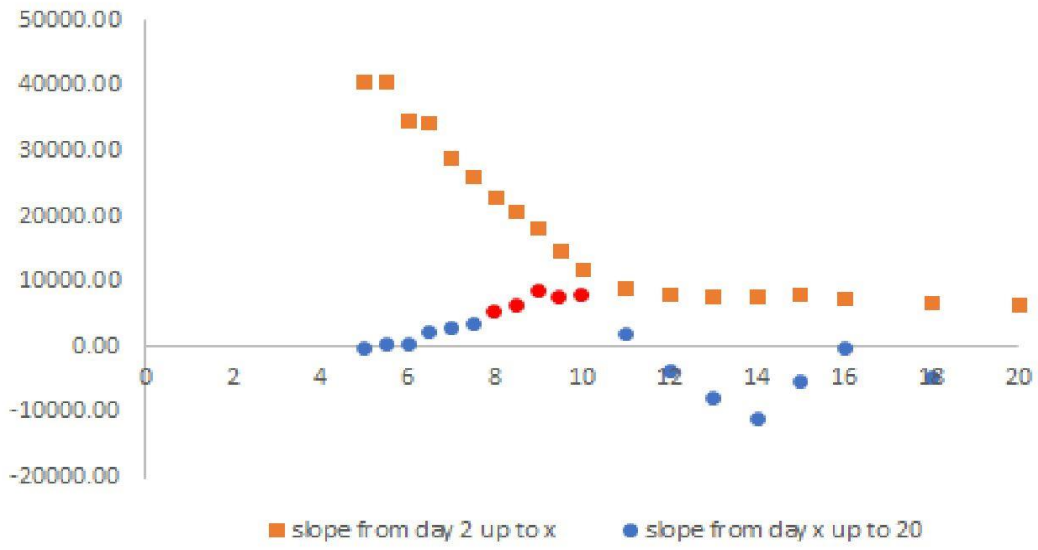


Figure 11. Slopes of linear regression models with egg size explained by mother's age in L2 lineage

Maternal age influences the egg size in a wide group of insect species, including Coleoptera (WASSERMAN and ASAMI 1985, FOX 1993), Lepidoptera (KARLSSON and WIKLUND 1984 and 1985, BRABY and JONES 1995), Orthoptera (CARRIERE and ROFF 1995), Diptera (WARREN 1924, JANN and WARD 1999, MCINTYRE and COODING 2000), Heteroptera (DIXON and WRATTEN 1971, NEWTON and DIXON 1990, KASULE 1991, MCLAIN and MALLARD 1991, HONEK 1992, DIXON et al. 1993), and Hymenoptera (AL-LAWATI and BIENEFELD 2009). According to the references from various authors, some data supports the

reduction of egg size over time with respect to maternal age (FOX 1993; YANAGI and MIYATAKE 2002). Some other authors have observed an increase in egg size with increasing maternal age (KASULE 1991). Some others emphasize that there are no significant differences in egg size with respect to maternal age (BERGER 1989, MARSHAL 1990). The most common explanation for this phenomenon is the resource depletion hypothesis, according to which it may be a physiological limitation of the females to produce offspring of the same size (BEGON and PARKER 1986, FOX 1993). The observed decrease in egg size with increasing maternal age has been proven in two related species of bruchid beetles, *Callosobruchus maculatus* (Fabricius) and *C. chinensis* (Fabricius) (Coleoptera) (FOX 1993, YANAGI and MIYATAKE 2002). Females with diminished resources for egg production laid smaller eggs with increasing maternal age, and those who were allowed to access food laid larger eggs even at later maternal ages. Alternatively, BEGON and PARKER (1986) proposed that the decrease in egg size with increasing maternal age may be adaptive when the female clutch size is constrained. However, our experiment was not designed to test such a hypothesis.

In *T. tabaci*, maternal age overall affected the egg size of both males and females produced by mated mothers in the L1 and T lineages throughout their lifespans. The egg size of males and females of both lineages decreased with increasing maternal age. As long as the maternal diet was not manipulated in this study, our results are not consistent with the resource depletion hypothesis. However, in the very young maternal age groups (3-5 day old mothers), 7-10 day old mothers, and older than 10 days, male and female egg size of mated mothers in both L1 and T lineages stayed at a constant level, without significant changes in egg size. While there is an increase in egg size at a very young maternal age (3-5 days) for male eggs produced by virgin mothers of the L1 and T lineages, this is not significant later in the age group of 7–10 days. Above 10 days old, the egg size of males produced by virgin mothers of the L1 lineage stayed at a constant level without changing egg size, and there is a decrease in egg size for male eggs produced by virgin mothers of the T lineage. In the case of the L2 lineage of the *T. tabaci* lineage, we can conclude egg size was linearly increasing with growing maternal age, but the rate of dependence (i.e., the slope of the trend) was decreasing up to day 10, and thereafter it did not change notably.

4.5. Morphometric analysis of *T. tabaci* species complex

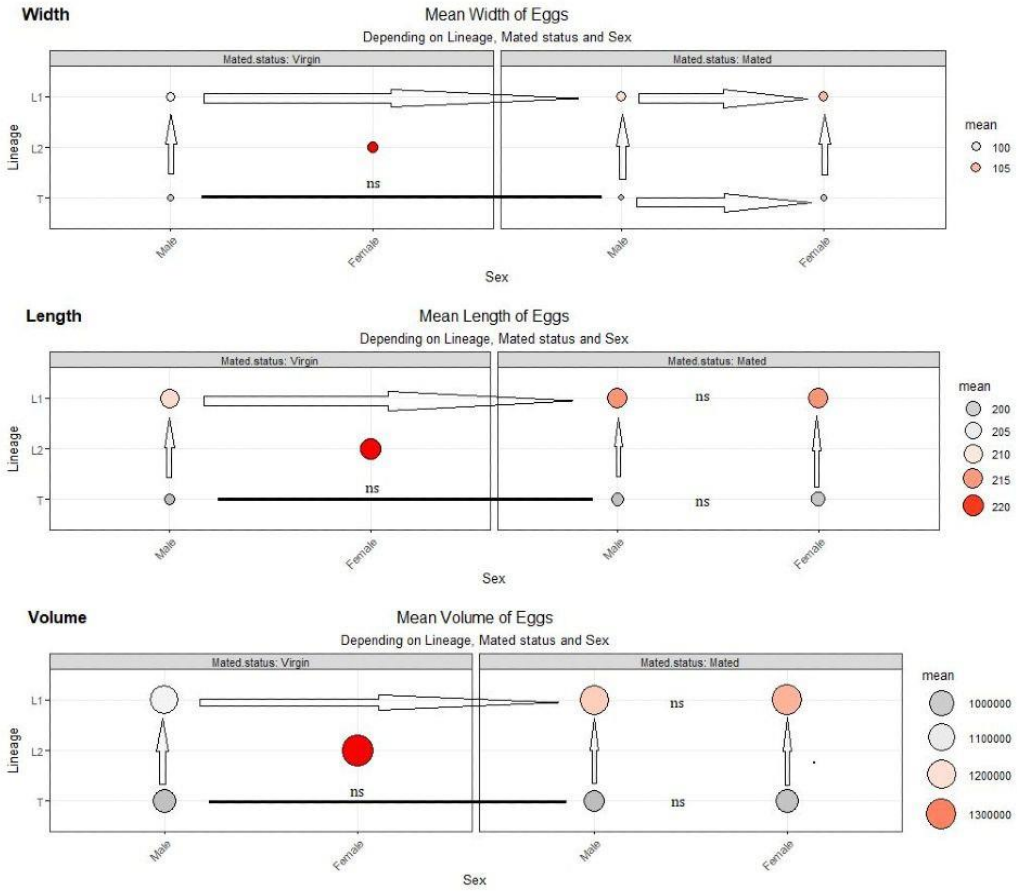
4.5.1. Morphometric analysis of eggs

According to three-way MANOVA, there were highly significant factor effects on the size of the eggs of *T. tabaci* (lineage: Wilk's $\lambda = 0.629$, $F(3, 3683) = 723.61$, $p < 0.001$; mated status: Wilk's

$\lambda = 0.991$, $F(3, 3683) = 10.97$, $p < 0.001$; sex: Wilk's $\lambda = 0.998$, $F(3, 3683) = 2.81$, $p < 0.05$; lineage*mated status interaction: Wilk's $\lambda = 0.989$, $F(3, 3683) = 13.80$, $p < 0.001$) with insignificant lineage*gender interaction ($p > 0.16$; Figure 12). The follow-up three-way ANOVA revealed highly significant lineage effects on all three parameters (width, length, and volume) ($F(1,3685) > 816.15$, $p < 0.001$) which showed significantly wider, longer, and greater L1 eggs compared to T eggs. The effect of mated status was significant on length and volume ($F(1,3685) > 16.92$, $p < 0.001$) and slightly significant (with Bonferroni's correction) on width ($F(1,3685) = 5.40$, $p = 0.06$). The effect of gender was significant on width and volume ($F(1,3685) > 7.13$, $p < 0.05$), but not on length ($F(1,3685) = 0.49$, $p = 0.48$).

Since the interaction of lineage and mated status was highly significant ($p < 0.001$), the factor levels of each factor were compared with the factor levels of the other two factors. It revealed that in the case of L1, all three parameters of male eggs from mated mothers were significantly greater than those of virgin mothers ($p < 0.001$). Meanwhile, the mated status effect was insignificant in the case of T eggs ($p > 0.05$). The width of female eggs laid by mated mothers was significantly higher than male eggs in the case of L1 and T lineages ($p < 0.001$), although a significant gender effect was not detectable for egg length and volume ($p > 0.05$, Figure 12).

Overall, considering all the groups of the three lineages of *T. tabaci*, the female eggs of the L2 (virgin) mothers were significantly larger than all the other groups, considering all three parameters ($p < 0.001$). These were followed by female and male eggs from mated mothers of the L1 lineage. Meanwhile, the egg size of the next group in magnitude, i.e., the male eggs of the virgin L1 mothers, is significantly bigger than the eggs of females and males of virgin and mated mothers of the T lineages, which are the three smallest groups among all groups of the three lineages (Figure 12).



	Mated status	Virgin		Mated	
	Gender / Lineage	Male (Mean±SE)	Female (Mean±SE)	Male (Mean±SE)	Female (Mean±SE)
Width (µm)	L1	101.16±5.34 (*N*=598)	⇒	*103.68±4.92* (*N*=91)	⇒ **105.00±4.31** (*N*=119)
	L2		109.26±3.97 (*N*=889)		
	T	96.85±4.08 (*N*=1558)	⇔	95.80±3.60 (*N*=112)	⇒ **96.61±3.47** (*N*=325)
Length (µm)	L1	210.79±7.86	⇒	*215.33±8.24*	⇔ 215.25±7.49
	L2	⇑	221.10±7.23	⇑	⇑
	T	195.88±7.95	⇔	196.50±8.11	⇔ 197.54±7.77
Volume (µm)³	L1	1132798±125927	⇒	*1215783±133761*	⇔ 1245540±120556
	L2	⇑	1384575±117827	⇑	⇑
	T	964036±93149	⇔	946061±85649	⇔ 966454±77236

Figure. 12 Comparisons of width (µm), length (µm), and volume (µm)^3 of male and female eggs of virgin and mated mothers of L1, L2, and T lineages of *T. tabaci.* Data are expressed as mean ± SD. *N* is the number of tested individuals. Means of significantly wider **female** eggs of mated L1 and T mothers (compared to **male** eggs of mated L1 and T mothers) are in bold. Means of significantly wider, longer, and greater L1 male eggs of *mated* mothers (compared to L1 male eggs of *virgin* mothers) are in italic. Means of significantly wider, longer, and greater eggs of L2 mothers (compared to all other eggs) are in red. L1 eggs are significantly wider, longer, and greater than T eggs when comparing male eggs of virgin mothers or male eggs of mated mothers. Arrows point in the direction of significantly greater values ($p<0.05$). Arrows with two heads are not significantly different values ($p>0.05$).

4.5.2. Morphometric analysis of first instar larvae and adults

The two principal components, PC1 and PC2, gained for *T. tabaci* larvae explain 86.7% of the total variation. PC1 is strongly and significantly positively correlated with variables D4 metanotum and D2 terg.VIII (that are highly significantly correlated with each other and also with D3 metanotum and D2 terg. II that were previously eliminated from the analysis); moreover, PC1 is moderately, although still significantly positively correlated with variable V3 stern. IX, (that is also positively correlated with D2 terg.VIII).

The correlation coefficients between the original (or transformed) variables and the PCs (i.e., the loadings) are shown in Table 13.

Table 13. Loading values of Principal Component Analysis (PCA) for the first two components (PC1 and PC2) in first instar larvae

Variables	PC1 (65.4%)	PC2 (21.3%)
D4 metanotum	**0.940**	0.138
D2 terg.VIII	**0.863**	0.278
V3 stern.IX	**0.487**	0.258
D3 head	0.156	**0.883**
transformed D3 pronotum	0.217	**0.929**
Standard deviation	1.809	1.031
Proportion of variance	0.654	0.213
Cumulative proportion of variance	0.654	0.867

Note: High loading values are in bold. See Figure 1 for the abbreviation

PC2 is strongly and significantly correlated to the variables D3 head and (transformed) D3 pronotum (that are highly correlated with each other and significantly and positively correlated with D4 head and (transformed) D7 pronotum).

In the direction of variables D4 metanotum, D2 terg.VIII and V3 stern.IX, (and also D3 metanotum and D2 terg.II,), the biggest is the L2 female, together with T lineage (females and males produced by virgin and mated mothers), followed by L1 females and L1 males produced by mated mothers, and the smallest ones are L1 males produced by virgin mothers. In this direction, T samples are very heterogeneous.

In the direction of variables D3 head and (transformed) D3 pronotum, (D4 head and (transformed) D7 pronotum,), the biggest is the L2 females followed by L1 females and L1 males produced by mated mothers. The smallest ones are those of the T lineage (females and males produced by virgin and mated mothers) together with L1 males produced by virgin mothers.

The morphometric variation of the first instar larvae of different groups of *T. tabaci* lineages ordinated by PCA is shown in Figure 13. Along PC1 and PC2, clear partitions are shown between L2 females and L1 males produced by virgin mothers and between L1 females and L1 males produced by virgin mothers.

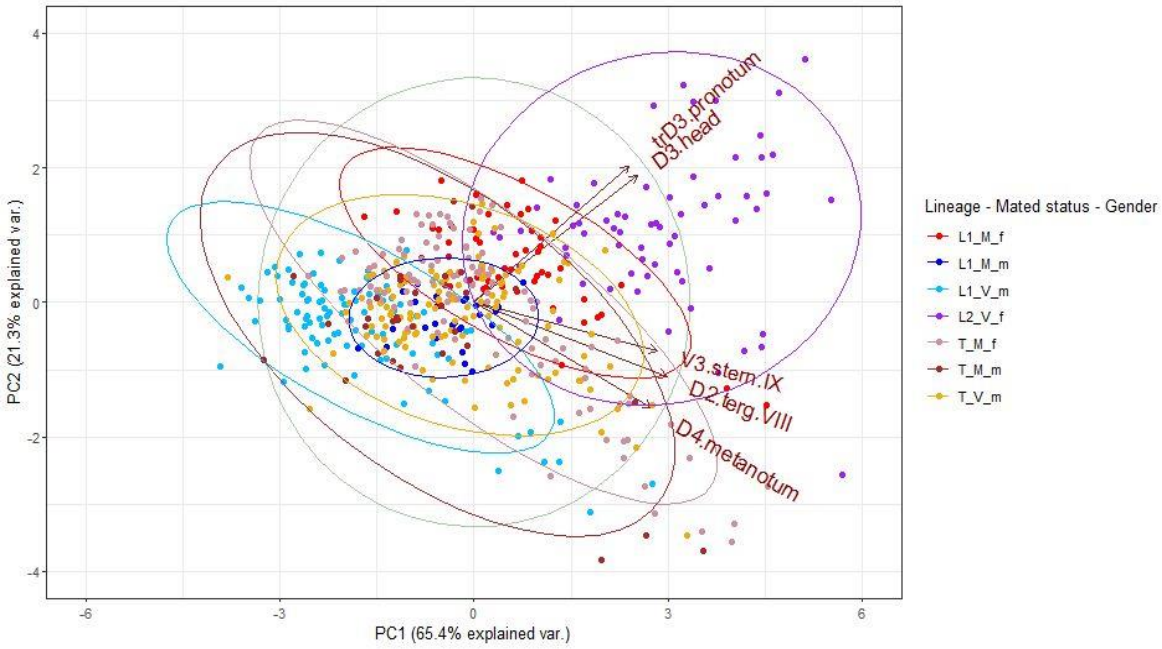


Figure 13. Principal Component Analysis biplot for the observed variables of larval size of different groups of *T. tabaci* lineages. Vector captions: D3 head, (transformed) D3 pronotum (trD3 pronotum), V3 stern.IX, D2 terg.VIII, D4 metanotum. Brown arrows represent the measured variables and ellipses of different colours represent the 95% confidence range around the sampling points relative to the lineage (L1, L2, T), mated status (V: virgin, M: mated), and gender (m: male, f: female).

The two principal components, PC1 and PC2, gained for *T. tabaci* adults explain 90.0% of the total variation (Table 14). PC1 is strongly and significantly positively correlated with variables P.a.s, Meta.s.1, Oc.s.2, and S2 terg.VIII and slightly (still significantly) with Meta.s.2 (that are also highly correlated with each other and with S2 terg.VIII, S3 terg.IV, and Discal.s.3, which were previously eliminated from the analysis).

PC2 is highly correlated with Oc.s.3 and slightly with Oc.s.2 and S2 terg.VIII (the two latter are significantly correlated with each other and with Discal.s.3 and S3 terg. IV that were previously eliminated from the analysis).

The correlation coefficients between the original (or transformed) variables and the PCs (i.e., the loadings) are shown in Table 14.

Table 14. Loading values of Principal Component Analysis (PCA) for the first two components (PC1 and PC2) in adults

Variables	PC1 (75.9%)	PC2 (13.6%)
P.a.s.	**0.896**	0.112
Meta.s.1	**0.859**	0.265
Oc.s.2	**0.782**	**0.486**
S2 terg.VIII	**0.770**	**0.440**
Meta.s.2	**0.476**	0.184
Oc.s.3	0.190	**0.963**
Standard deviation	2.134	0.904
Proportion of variance	0.764	0.136
Cumulative Proportion	0.764	0.900

Note: High loading values are in bold. See Figure 1 for the abbreviation.

The result of PCA conducted on adult measurements is shown in Figure 14. The visualization of the results of the PCA suggested a clear separation between females of T and L lineages, but L1 and L2 cannot be separated according to the measured characters. Regarding the males of the L1 and T lineages, we detected that it does not make a meaningful difference whether they are produced by virgin or mated mothers. However, a notable difference can be detected between L1 and T males. Both lineages are relatively low in all the characters, though T samples have even lower values than L1. The difference between them is higher considering Oc.s.3. The only parameter that is slightly higher in T lineage is P.a.s.

Along the PC1, clear partitions are shown between L1 females from all other groups except L2 females. Along PC2, slighter partitions are shown between females of L1 and T lineages and females of the L2 and T lineages.

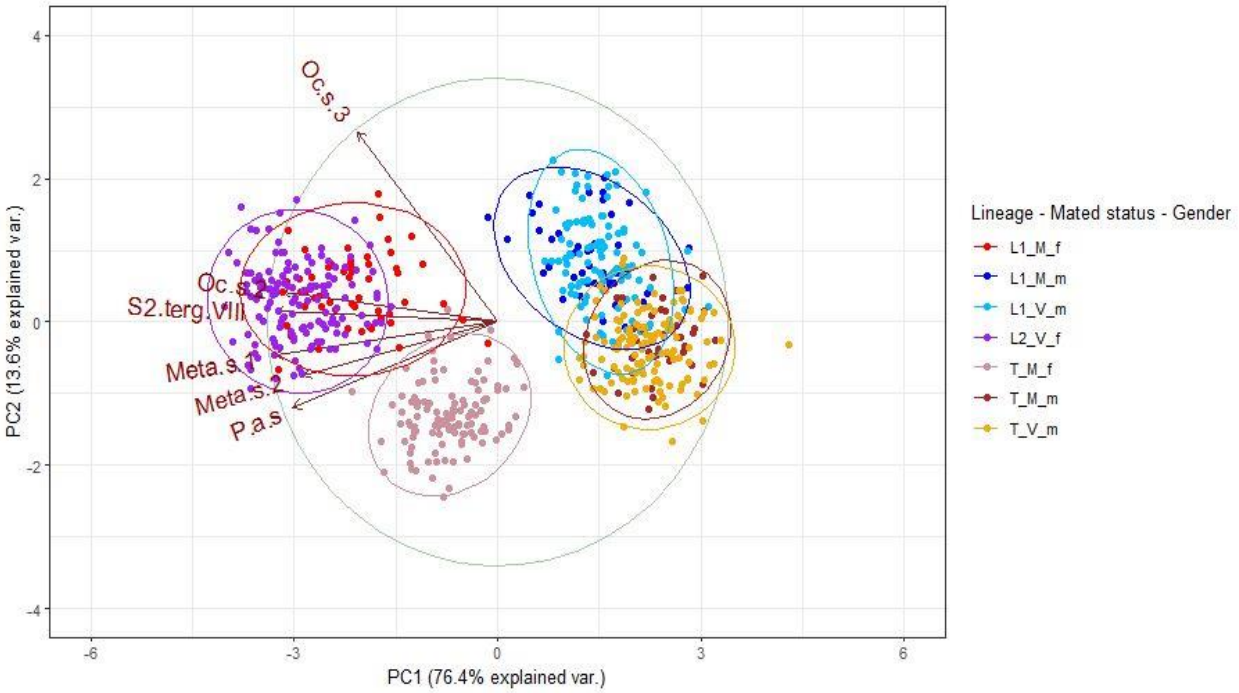


Figure 14. Principal Component Analysis biplot for the observed variables of the adults of different *T. tabaci* lineages. Brown arrows captions: Oc.s.3, P.a.s, Meta.s.1, Meta.s.2, Oc.s.2, S2 terg.VIII. Brown arrows represent the measured variables, and ellipses of different colours represent sampling points relative to the lineage (L1, L2, T), mated status (V: virgin, M: mated), and gender (m: male, f: female).

A morphometric measurement is an effective tool that has been used for the identification, determination of larval instars, and discrimination of cryptic species. In a former study conducted on different populations of *T. tabaci*, the morphological distinction of the adults was shown between the populations collected from tobacco and onion fields in Iran (FEKRAT et al. 2014). Our study indicates that morphometric measurements of the eggs are very important in discriminating between females of L1, L2, and T lineages and between the males of L1 and T lineages. The PCA analysis conducted on morphometric measurements of the first instar larvae and the adults of different groups of the three lineages of *T. tabaci* suggests a clear separation between female adults of T from those of L lineages of *T. tabaci*, as was reported by FEKRAT et al. (2014), but not in the first instar larvae. This study supports the existence of two different lineages based on the morphometric measurements, as was first proposed by ZAWIRSKA (1976). The most important character that explains most of the variation in the adult female is the distance between the third ocellar setae of the head.

The morphometric analysis method used in this study for discriminating between lineages of *T. tabaci* requires a prior species identification method, especially when *T. tabaci* specimens are collected from the field, which may include other thrips species. Other *Thrips* spp., such as the *T. hawaiiensis* species group (PALMER and WETTON 1987), *Thrips parvispinus* Karny (JOHARI et al. 2014), and two morphologically similar thrips species, *Thrips fuscipennis* Haliday and *Thrips sambuci* Hegger (FEDOR et al. 2014), exhibit morphometric variations as well. Therefore, the discrimination of *T. tabaci* lineages based only on morphometric analysis may lead to misidentification in potentially mixed field-collected samples.

Moreover, a clear separation between males and females is shown in the adult stage but not in the first instar larvae of both the L1 and T lineages. Traits that explained most of the variation between males and females of the L1 and T lineages in the adult stage were the distance between the inner posteroangular setae of the pronotum, the distance between the lateral and median metanotal setae, the distance between the second ocellar setae of the head, and the distance between dorsal setae two of abdominal tergite VIII.

Sexual size dimorphism is a common phenomenon in insect taxa where both sexes differ in body size (SHINE 1989). There are different explanations for how sexual size dimorphism arises in insects, and most of them rely on the ontogeny of males and females. In particular, it is often unclear if the individuals of the ultimately larger sex are already larger at hatching/birth if they grow faster, or if they grow for a longer time. BLANCKENHORN et al. (2007) found that in four out of seven studied arthropod taxa with female-biased sexual size dimorphism, the difference between growth rates in sexes is more important than the difference in developmental time. It has also been shown that the female larvae develop from larger eggs than male larvae do; thus, the female has a larger size from the very beginning of its development and maintains the size differences during the whole ontogeny (BUDRIENE et al. 2013).

In this study, there is no egg size sex difference in both the L1 and T lineages produced by mated mothers of *T. tabaci*. The differences were not significant, either, in our first study, where the sex allocation in arrhenotokous lineages of *T. tabaci* was not mediated by egg size. Moreover, this study shows that males and females do not exhibit any size differences in the first instar larvae. The differences became visible later in the adult stage, where males and females of both L1 and T lineages are very well separated and located on opposite sides of the PCA biplot. In this respect, we can presume that the formation of the sexual size dimorphism in both lineages of *T. tabaci* may be

attributed to the different growth rates of males and females. To our knowledge, no studies of insect eggs have found differences in eggs that develop into different sexes.

On the other hand, some investigations in birds explain that adult size can be independent of egg size. RUTKOWSKA et al. (2014) published evidence that egg sexual size dimorphism does not predict adult sexual size dimorphism across species. For instance, in the spotless starling, *Sturnus unicolor*, males are bigger at the adult stage even though they hatched from smaller eggs (CORDERO et al. 2001). In some other species, like brown songlark *Cinclorhamphus cruralis*, although male adults are bigger than females, they hatched from smaller eggs (MAGRATH et al. 2003). In the American kestrel, *Falco sparverius*, female adults are larger than males; yet, females hatch from smaller eggs than males (ANDERSON et al. 1997).

5. CONCLUSIONS AND RECOMMENDATIONS

1. The fact that larger eggs are more likely to hatch than smaller eggs in the L1 lineage laid by mated mothers and in the T lineage of *T. tabaci* for all eggs, independently of mating status, indicates that egg size might be a predictor of energy content in some cases. Mating also affected the hatching probability of the eggs in the L1 lineage, with more eggs hatching from virgins than from mated mothers; and in the T lineage, mating did not affect the hatching probability of the eggs.

2. Sex allocation in haplodiploid *T. tabaci* is not mediated by egg size like in *Tetranychus urticae* and *Pezothrips kellyanus*. Egg size and gender were independent of maternal age in the L1 lineage, while in the T lineage, the observed egg size difference between males and females was only present in the progeny of young females (7–10-day-old mothers). Our results demonstrate that studying the relationship between egg size and gender in a narrow age group of mothers might lead to misconclusions unless different mechanisms are working in mated females depending on their age. Moreover, this study rise the need for further testing this process in other haplodiploid species.

3. Eggs laid by mated mothers were significantly larger than eggs laid by virgin mothers throughout their lifespan and in all other age groups in the L1 lineage. The mean value of the egg size distribution of mated mothers in the L1 lineage was larger than that of virgins throughout their lifespan. This suggests that no egg size determines fertilization in this lineage, rather, it is fertilization that may influence egg size. Eggs produced by mated mothers receive more resources than those produced by virgins, and mating just increases egg size in general, thus leading to a larger size of male eggs produced by mated mothers than by virgins (Figure 2B, scenario 2). Contrary to the L1 lineage, in the T lineage, an entirely new scenario is needed to assess the obtained results; eggs laid throughout the lifespan of virgin mothers were significantly larger than those of mated mothers.

4. Egg size decreases with increasing maternal age in the L1 and T lineages of *T. tabaci* and this cannot be attributed to the resource depletion hypothesis. In the case of the L2 lineage of *T. tabaci* lineage, we can conclude that egg size was linearly increasing with growing maternal age, but the rate of dependence (i.e., the slope of the trend) was decreasing up to day 10, and thereafter it did not change notably.

5. Morphometric measurements were used to discriminate between lineages of *T. tabaci.* The results revealed significant differences in egg size between the three lineages. Female eggs of the L2 (virgin) mothers were larger than all the other groups. These were followed by female and male eggs from mated mothers of the L1 lineage. Meanwhile, the size of the male eggs of the virgin L1 mothers is bigger than the eggs of females and males of virgin and mated mothers of the T lineages, which are the three smallest groups among all groups of the three lineages.

6. Females of the L and T lineages are different in size from each other in the adult stage but not in the first instar larval stage. The character that explains most of the variation is ocellar setae three. The morphometric analysis used in this study for discriminating between lineages of *T. tabaci* requires a prior species identification method, especially when thrips specimens are collected from the field, which plausibly may include other thrips species that exhibit morphometric variation as well. Therefore, the discrimination of *T. tabaci* lineages based only on morphometric variation may lead to misidentification in potentially mixed field collected samples.

7. Adult sexual size dimorphism in L1 and T lineages is not mediated by the size of the eggs and newly hatched first instar larvae, but the different growth rates of males and females results in sexual dimorphism in the adult stage.

6. NEW SCIENTIFIC RESULTS

1. Larger eggs are more likely to hatch than smaller eggs in the L1 lineage laid by mated mothers and in the T lineage of *T. tabaci* for all eggs independently from mating status.

2. Our results provide the first empirical evidence that egg size has no influence on sex allocation in this haplodiploid species and urges for further testing of this process in other haplodiploid species.

3. Eggs produced by mated mothers were larger than eggs produced by virgin mothers in the L1 lineage. In the T lineage, eggs produced by virgin mothers were larger than those of mated mothers. Our findings indicate that these two subspecies of *T. tabaci* have different resource allocation strategies in response to maternal mating status.

4. Male eggs produced by mated mothers were larger than those produced by virgin mothers in the L1 lineage, but in the T lineage, there were no differences in the size of male eggs produced by mated and virgin mothers.

5. The overall decreasing effect of increasing maternal age on egg size within both genders of the L1 and T lineages cannot be attributed to the resource depletion hypothesis, whereas in the L2 lineage, there is an increase in egg size with increasing maternal age.

6. The female eggs of the L2 lineage were larger than those of the two other lineages.

7. The size of females of the L and T lineages is well separated from each other in the adult stage but not in the first instar larva.

8. Adult sexual size dimorphism in L1 and T lineages is not mediated by the size of eggs and first instar larvae but by different growth rates of males and females.

7. SUMMARY

How parents control the sex of their offspring differs greatly in the Animal Kingdom. Two lineages in the *Thrips tabaci* Lindeman cryptic species complex exhibit arrhenotokous haplodiploidy, which enables parents to influence the sex of offspring by different fertilization mechanisms. Since in two other haplodiploid species, sex allocation was found to be mediated by egg size, we tested this mechanism in the L1 and T lineages of *T. tabaci*. Contrary to the two haplodiploid arthropods with an egg-size-mediated sex allocation mechanism, our study proves that a different mechanism regulates sex allocation in *T. tabaci* that is independent of the size of eggs. Egg size and gender were independent of maternal age in the L1 lineage, whilst in the T lineage, the observed egg size difference between males and females was only present in the progeny of young females (7–10-day-old mothers). Our results demonstrate that studying the relationship between egg size and gender in a narrow age group of mothers might lead to misconclusions unless different mechanisms are working in mated females depending on their age.

By comparing the size of eggs produced by virgin and mated mothers, we showed that mated females laid significantly larger eggs throughout their lifespan and in all other age groups in the L1 lineage. The mean value of the egg size distribution of mated mothers in the L1 lineage was larger than that of virgins throughout their lifespan. This may suggest that no egg size determines fertilization in this lineage but rather that fertilization may influence egg size. Eggs produced by mated mothers might receive more resources than those produced by virgins, and mating just increases egg size in general, thus leading to a larger size of male eggs produced by mated mothers than by virgins (Figure 2B, scenario 2). Contrary to the L1 lineage, in the T lineage, an entirely new scenario is needed to assess the obtained results; eggs laid throughout the lifespan of virgin mothers were marginally larger than those of mated mothers.

We have found that maternal age has an overall effect on the size of both males and females produced by mated mothers in the L1 and T lineages throughout their lifespan. Since the maternal diet was not manipulated in this study, our results are not consistent with the resource depletion hypothesis. However, in the very young maternal age group (3–5-day-old mothers), 7–10-day-old mothers, and older than 10 days, male and female egg sizes of males and females produced by mated mothers in both L1 and T lineages stayed at a constant level, without significant changes in egg size. In the case of the L2 lineage of *T. tabaci* lineage, we can conclude that egg size was linearly increasing

with growing maternal age, but the rate of dependence (i.e., the slope of the trend) was decreasing up to day 10 and thereafter it did not change notably.

There is no known morphological difference between the adults of the three lineages of *T. tabaci*. The most accurate method for identifying the lineages of *T. tabaci* is based on molecular identification. Therefore, we investigated the morphometric variability of the egg size, first instar larva, and adult size to identify characters that may be useful in discriminating the lineages. From morphometric measurements of the eggs, we discovered that there are differences in the size of the eggs between lineages of *T. tabaci*. The female eggs of the L2 lineage were larger than those of the two other lineages. These were followed by male and female eggs of the L1 lineage. While male and female eggs of the T lineage were the smallest among lineages of *T. tabaci*. This supports the existence of three different lineages. We also discovered that females of the L and T lineages are morphologically different from each other in the adult stage but not in the first instar larval stage.

With regards to the size of the L1 and T lineages, we proved that adult sexual size dimorphism in the L1 and T lineages is not mediated by the size of the eggs and newly hatched first instar larvae but by the different growth rates of males and females.

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