Hungarian University of Agriculture and Life Sciences

Biological, Ecological and Behavioural Aspects of Onion thrips (*Thrips tabaci* Lindeman, 1889) Species Complex

Doctoral (PhD) Dissertation

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1. INTRODUCTION

Onion thrips, *Thrips tabaci* LINDEMAN, 1889, is a polyphagous insect pest for many agricultural and horticultural crops worldwide (GILL et al. 2015). The origin of the ancient *T. tabaci* is unknown. Although, some researchers believe that most probably the species originates from eastern Mediterranean where its favoured host plant *Allium cepa* LINNAEUS, 1753, is derived (MOUND 1997). *T. tabaci* was first described based on specimens collected from onion, *Allium cepa* L, cabbage, *Brassica oleracea* L.; cucumber, *Cucumis sativus* L.; and parsley, *Petroselinum crispum* L. in 1888 (LINDEMAN 1889). Since then, its distribution has increased worldwide and it became a key pest of agricultural crops (MOUND and WALKER 1982). PERGANDE (1895) in North America identified *T. tabaci* correctly for the first time in the early 1890s.

Thrips tabaci was recognized as a single thrips species before ZAWIRSKA (1976) described different biological types. Based on reproductive modes, host adaptations, virus transmission efficiency *Tomato spotted wilt virus* (TSWV), and morphological differences on the abdominal tergites of second-stage larvae she has proposed two distinctly different forms of *T. tabaci* types, namely, communis and tabaci types. Communis type had arrhenotokous reproductive mode (males produced from unfertilized eggs and females produced from fertilized eggs), and thelytokous reproductive mode (females produced from unfertilized eggs), broad host plants, less virus transmission efficiency, whereas tabaci had only arrhenotokous reproductive mode, a small group of host plants and high virus transmission efficiency. Since then, based on DNA sequences of the Mitochondrial Cytochrome c oxidase I (mt COI) genes, *T. tabaci* has been cleavaged into three lineages: two leek-(L1, L2) and tobacco-associated (T) (BRUNNER et al. 2004, TODA and MURAI 2007), KOBAYASHI and HASEGAWA 2012, JACOBSON et al. 2013, KOBAYASHI et al. 2013, FEKRAT et al. 2014. The leek-associated (L1) is the ancient form of *T. tabaci*. It is believed that tobacco-associated (T) type diverged from the ancient form of L1 and since then adapted to solanaceous host plants (BRUNNER et al. 2004). *T. tabaci* lineages exhibits three distinictive reproductive biology such as arrhenotokous (males produced from unfertilized eggs and females produced from fertilized eggs) (HARRIS et al. 1935); thelytokous (females produced from unfertilized eggs) (EDDY and CLARKE 1930, SAKIMURA 1932, 1937) and deuterotokous (both females and males produced from unfertilized eggs) deuterotokous (NAULT et al. 2006).

Both adults and larvae of *T. tabaci* cause damage to their hosts by piercing the surface tissues and sucking the contents of plant cells, which results in small silvery patches that turn into white blotches. This damage reduces the photosynthetic capacity of plants, which caused tip

dieback, curling, and twisting of leaves (LEWIS 1973). In addition to direct damage to the crops, *T. tabaci* is a vector for different plant viruses including (TSWV) (PITTMAN 1927, MACHARIA et al. 2015), *Iris yellow spot virus* (IYSV) (CORTÊS et al. 1998, HSU et al. 2010, WIJKAMP et al. 1995), *Tomato yellow ring virus* (TYRV) and *Alstroemeria yellow spot virus* (AYSV) (ROTENBERG et al. 2015, HASSANI-MEHRABAN et al. 2019). The exact economic losses are uncertain but due to its polyphagous nature and vector of several plant viruses, its damage has been estimated to cause more than U.S. $1 billion in crop losses annually worldwide (BALAN et al. 2018).

The risk of large economic losses due to the infestation of protected and field crops by *T. tab*aci requires the use of control measures. The most common method to control *T. tabaci* is the use of foliar insecticides, but *T. tabaci* is difficult to control because the mobile stages of this pest found mainly in the narrow spaces between the inner leaves where spray coverage is difficult. In addition, the eggs are laid into the leaf tissues where they may escape from the control. Reinfestation of crop fields can occur from the surrounding non-crop vegetation and immigration of *T. tabaci* from nearby fields. Moreover, due to its polyphagous nature, cryptic habits, small size, and presence of various reproduction mode, some populations of *T. tabaci* have developed resistance to insecticides in several parts of the world (MARTIN et al. 2003, SHELTON et al. 2003, MACINTYRE et al. 2005, MORISHITA 2008). Recent research in Europe and North America has concentrated on understanding the biological, behavioural and ecological aspects of *T. tabaci* so that any chosen control method can be targeted more efficiently against the pest. At this time, very little research has done on *T. tabaci* as cryptic species complex worldwide. This Ph.D project combines researches regarding the ecological, biological, and behavioural aspects of *T. tabaci* lineages in the laboratory in order to improve our knowledge, and ability to control *T. tabaci* lineages outbreaks.

2. OBJECTIVES

The overall aim of this Ph. D research was to investigate the biological, ecological, and behavioural aspects of *T. tabaci*. A better understanding of the biology, ecology, and behaviour of *T. tabaci* lineages could be contributed to the development of better management practices under field or greenhouse conditions: it will allow farmers to specifically select crops grown in a rotation that disrupt the life cycle of this pest.

The main proposed specific researches were:

1. Study the reproductive diapause of *T. tabaci* lineages at different temperature and photoperiod levels. The aim of this research was to measure the effect of temperature and photoperiod on the pre-oviposition, reproductive diapause, oviposition, longevity and fecundity of *T. tabaci* lineages.
2. Study the inbreeding depression and its effects on the different lifetable parameters and sex ratio of the arrhenotokous lineages of the *T. tabaci* lineages. The aim of this research was to compare the lifetable parameters (fecundity, egg hatchability rate, longevity and sex ratio) of L1 and T lineages that underwent brother and sister for the consecutive generations.
3. Examine the influence of temperature on the sex ratio of the leek- (L1) and tobacco-associated (T) lineages. The aim of this research was to investigate the effect of temperature on the sex ratio and life table parameters of leek - (L1) and tobacco – associated (T) lineages. The study of sex ratio and their sympatric variation is necessary for realizing of causes and results in the variations of population structures and mating systems.
4. The existence of deuterotokous reproduction mode in the *T. Tabaci* lineages. The aim of this research was to reveal if adult males could fertilize immature female pupae in the arrhenotokous L1 and T lineages and to identify if the mother to son inbreeding could induced deuterotokous reproductive mode.
5. Test the male fighting behaviours of L1 and T lineages. The aim of this research was to characterize the male fighting behaviour and to compare the fighting performance at different ages of males in the L1 and T lineages.

3. LITERATURE OVERVIEW

3.1. Onion thrips, classification, identification, morphology and reproductive biology

3.1.1. Classification

Thrips tabaci belong to the order Thysanoptera, suborder Terebrantia, family Thripidae, subfamily Thripinae and genus Thrips (MURAI et al. 2002). *T. tabaci* was first described by a Russian entomologist, Karl Eduard Lindeman and caused severe damage to tobacco plants (LINDEMAN 1889). *T. tabaci* is believed to be a native of the eastern Mediterranean, from where its favoured host plant *Allium cepa* LINNAEUS, 1753 is derived (MOUND 1997). *T. tabaci* is characterized by its fringed wings, from which its scientific name has been derived Thysanoptera (LEWIS 1973). This pest is very small creatures that can easily spread in large areas without even being noticed. Based on this reality, *T. tabaci* is a cosmopolitan thrips species (LEWIS 1973).

3.1.2. Identification

Thrips tabaci is a cosmopolite and polyphagous thrips species, and its precise identification from other related species is the fundamental step to develop genetic and other biological information that is necessary for designing effective pest and vector management. The identification of *T. tabaci* is primarily dependent on morphological characters such as colour, chaetotaxy, body architecture. However, their minute size and cryptic behaviour, sexual dimorphism, high degree of similarity in various developmental stages, and polymorphism (in colour, wing development, body size) onion thrips raise two taxonomic problems for morphology-based identification to detect in the field, i.e. the identification of closely related thrips species and identification of different forms of *T. tabaci* lineages. Therefore, to design effective treatments against *T. tabaci*, it is necessary to develop reliable and accurate identification methods. To this day, the identification methods of onion thrips are in accordance with their external morphological and molecular characteristics. A conjunction of these two methods gives rise to the most reliable identification across all life stages of onion thrips.

Morphological characteristics of onion thrips

Adult onion thrips vary in body colour and size depending on environmental temperature during their developmental time. The high temperature usually induces fast-growing, small and pale yellow, and low-temperature induces slow-growing, large and dark brown thrips (SAKIMURA 1937, MURAI et al. 2002). Microscopic keys are often based on written

descriptions of contrasting characters such as the number of antennal segments and the distribution and number of setae across the body and along the forewings (**Table** 1).

Table 1: List of morphological characteristics that collectively distinguish *T. tabaci* from other species in the genus thrips (MOUND and MASUMOTO 2005).

1	Antennae 7-segmented; segments III–IV with short forked sensorium, VII short
2	Body size and colour variable depending on temperature during development, from small and whitish yellow to large and brown
4	Ocellar pigment is usually grey, never red
5	Head wider than long; with 2 pairs of ocellar setae; pair III small, arising on anterior margins or just within ocellar triangle
6	all postocular setae subequal in length
7	Pronotum with 2 pairs of prominent posteroangular setae; posterior margin with 3 (sometimes 4) pairs of setae
8	Metanotum variable, usually irregularly reticulate medially with lines converging to midpoint at posterior margin; median setae short, arising behind anterior margin; campaniform sensilla absent
9	Fore wing first vein usually with 4 (varying 2-6) setae on distal half; second vein with about 15 setae
10	Abdominal tergite II with 3 lateral marginal setae; V-VIII with paired ctenidia, on VIII posteromesad to spiracles; tergite VIII posteromarginal comb complete, microtrichia long and slender; pleurotergites without discal setae, with closely spaced rows of fine ciliate microtrichia
11	Sternite II with 2 pairs of marginal setae, III-VII with 3 pairs; sternites without discal setae
12	Male: narrow transverse glandular area on abdominal sternites III-V only

Molecular Identification

Even though it is possible to discriminate onion thrips from other related thrips species, due to their small body size and inconspicuous morphological differences, it is hard or impossible to differentiate the different forms of *T. tabaci* lineages based on only morphological differences. To avoid such difficulty the use of molecular genetic techniques particularly the analysis of DNA sequences of the mitochondrial Cytochrome c oxidase I (mtCOI) gene has gained wide acceptance as a supplementary method to resolve taxonomic ambiguities, and the identification of cryptic species complex of *T. tabaci* (FARKAS et al. 2020) (**Figure** 1).

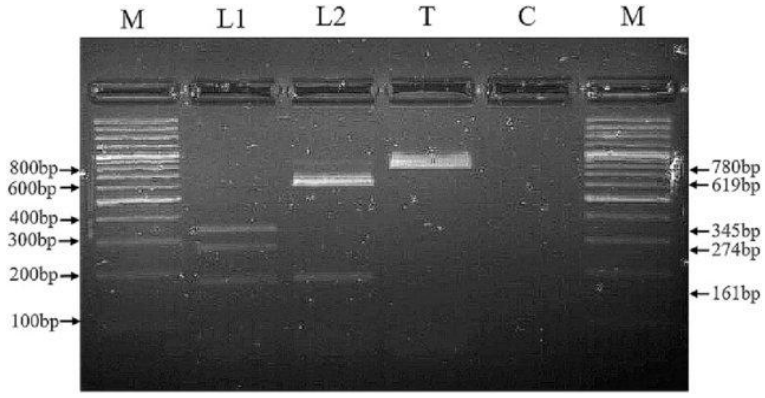

Figure 1: Restriction fragment patterns of the amplified mtCOI gene of T. tabaci digested with PsuI and PsyI endonucleases (FARKAS et al. 2020). Lane M is a 100 bp DNA ladder size marker. L1: three fragments of leek-associated arrhenotokous lineage after digestion (345 bp/274 bp/161 bp), L2: two fragments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

3.2. Reproductive biology and sex determination

Arrhenotokous and thelytokous reproductive modes are a common phenomenon in many thrips species in the world (**Table** 2). However, deuterotokous reproductive mode is a relatively uncommon phenomenon for thrips species since it has been reported only for *Apterothrips apteris* (Daniel) (STRAUSS and KARBAN 1995 and *T. tabaci* NAULT et al. 2006,). *T. tabaci* lineages exhibits three distinctive reproductive biology, i.e. arrhenotokous (L1 and T) (HARRIS et al. 1935); thelytokous (L2) (EDDY and CLARKE 1930, SAKIMURA 1932, 1937), and uncommonly deuterotokous (L1 and T) (NAULT et al. 2006).

Table 2: Lists of thrips species with different reproductive modes

Thrips species	**Reproductive biology**	**Authors and years**
Aeolothrips vittatus	Thelytoky	MORISON 1947
Akainothrips citritarsus	Arrhenotoky	WRENSCH and EBBERT 1993
Anaphothrips obscurus	Thelytoky	MORISON 1947
Anaphothrips striatus	Arrhenotoky	RISLER and KEMPTER 1961
Anthothrips niger	Arrhenotoky	RISLER and KEMPTER 1961
Apterothrips apteris	Arrhenotoky Thelytoky Deuterotoky	STRAUSS and KARBAN 1995
Aptinothrips rufus	Arrhenotoky	MORISON 1947, SHARGA 1933
Caliothrips indicus	Thelytoky	ANANTHAKRISHNAN 1990
Caliothrips fasciatus	Arrhenotoky	RUGMAN-JONES et al. 2012, LEWIS 1973
Chirothrips manicatus	Arrhenotoky	RISLER and KEMPTER 1961

Continuation of table 2		
Thrips species	**Reproductive biology**	**Authors and years**
Chirothrips mexicanus	Arrhenotoky	ANANTHAKRISHNAN, 1990, DANIEL 1981
Chaetanaphothrips orchidii	Arrhenotoky Thelytoky	LEWIS 1973
Echinothrips americanus	Arrhenotoky	LI et al. 2012
Euthrips tritici	Arrhenotoky	RISLER and KEMPTER 1961
Frankliniella fusca	Arrhenotoky	NEWSOM 1953
Frankliniella insularis	Arrhenotoky	DAVIDSON and BALD 1931
Frankliniella occidentalis	Arrhenotoky	WANG et al. 2014
Frankliniella schultzei	Arrhenotoky Thelytoky	GIKONYO et al. 2016
Frankliniella tritici	Arrhenotoky	ANANTHAKRISHNAN 1990
Gynaikothrips ficorum	Arrhenotoky	WRENSCH and EBBERT 1993
Haplothrips niger	Arrhenotoky	LOAN and HOLDAWAY 1955
Haplothrips subtilissimus	Thelytoky	PUTMAN 1942
Haplothrips niger	Arrhenotoky Thelytoky	ANANTHAKRISHNAN 1990
Haplothrips simplex	Arrhenotoky	PACCAGNINI et al. 2006
Haplothrips statices	Arrhenotoky	ANANTHAKRISHNAN 1990
Haplothrips statices	Arrhenotoky	RISLER and KEMPTER 1961
Haplothrips tritici	Thelytoky	ANANTHAKRISHNAN 1990
Haplothrips verbasci	Arrhenotoky	LEWIS 1973
Heliothrips haemorrhoidalis	Thelytoky Arrhenotoky	MORISON 1947, LEWIS 1973, HAN et al. 2011, HAMILTON 1967
Helionothrips errans	Thelytoky	LEWIS 1993
Hercinothrips femoralis	Thelytoky	KUMM and MORITZ 2008
Hoplothrips pedicularius	Arrhenotoky	OTTE 1979, WRENSCH, EBBERT 1993
Hoplothrips fungi	Arrhenotoky	WRENSCH and EBBERT 1993
Hoplothrips ulmi	Arrhenotoky	OTTE 1979
Katothrips tityrus	Arrhenotoky	WRENSCH and EBBERT 1993
Kladothrips rugosis	Arrhenotoky	WRENSCH and EBBERT 1993
Koptothrips dyskritus	Arrhenotoky	WRENSCH and EBBERT 1993
Koptothrips flavicornis	Arrhenotoky	WRENSCH and EBBERT 1993
Kurtomathrips morilli	Thelytoky	ANANTHAKRISHNAN 1990
Leucothrips nigripennis	Thelytoky	LEWIS 1993

Continuation of table 2		
Thrips species	**Reproductive biology**	**Authors and years**
Limothrips cerealium	Arrhenotoky	SHARGA 1933
Limothrips denticornis	Arrhenotoky	WRENSCH and EBBERT 1993, HAMILTON 1967
Microcephalothrips abdominalis	Arrhenotoky	ANANTHAKRISHNAN 1990
Onychothrips arotrum	Arrhenotoky	WRENSCH and EBBERT 1993
Oncothrips tepperi	Arrhenotoky	WRENSCH and EBBERT 1993
Onychothrips tepperi	Arrhenotoky	WRENSCH and EBBERT 1993
Parthenothrips dracaenae	Arrhenotoky Thelytoky	ANANTHAKRISHNAN 1990, MORISON 1947b
Pseudoarticulella obscurus	Thelytoky	MORISON 1947
Rhipiphorothrips cruentatus	Arrhenotoky	ANANTHAKRISHNAN 1990
Rhopalothripoides froggatti	Arrhenotoky	WRENSCH and EBBERT 1993
Sciothrips cardamom	Arrhenotoky	ANANTHAKRISHNAN 1990
Scirtothrips bispinoslls	Arrhenotoky	ANANTHAKRISHNAN 1990
Scirtothrips citri	Arrhenotoky	LEWIS 1973
Scirtothrips dorsalis	Arrhenotoky	ANANTHAKRISHNAN 1990
Scirtothrips longipennis	Thelytoky	LEWIS 1993
Scirtothrips perseae	Arrhenotoky	HODDLE 2002
Scolothrips sexmaculatus	Arrhenotoky	COVILLE and ALLEN 1977
Taeniothrips vulgatissimus	Arrhenothrips	LEWIS 1993
Taeniothrips inconsequens	Arrhenotoky	DAVIDSON and BALD 1931
Thrips linarius	Arrhenotoky	LEWIS 1973
Thrips nigropilosus	Arrhenotoky Thelytoky	NAKAO 1998
Thrips calcaratus	Thelytoky	PARKER et al. 1995
Thrips tabaci	Arrhenotoky Thelytoky Deuterotoky	HARRIS et al. 1935 EDDY and CLARKE 1930, SAKIMURA 1932,1937, NAULT et al. 2006
Warithrips maelzeri	Arrhenotoky	WRENSCH and EBBERT 1993
Xaniothrips leukandrus	Arrhenotoky	WRENSCH and EBBERT 1993
Xaniothrips xantes	Arrhenotoky	WRENSCH and EBBERT 1993
Zaniothrips ricini	Arrhenotoky	ANANTHAKRISHNAN 1990

Arrhenotokous haplodiploidy, paternal genome elimination, and thelytoky sex determinations have been reported in all thrips species, some hemipteran species, and several clades of beetles and mites (FILIA et al. 2015).

3.2.1. Arrhenotokous haplodiploidy

Arrhenotokous haplodiploid is the most common sex determination system for Thysanoptera, Hymenoptera insect order, and all members of Acariformes (FILIA et al. 2015). It has been estimated to occur in about 20% of all named species of animals (CROZIER and PAMILO 1996). In this sex-determination system, males are produced asexually which is termed as haploid, and females are produced sexually which is termed as diploid (RISLER and KEMPTER 1961). Males do not develop by the meiosis cell division process and carry haploid genome from their mother (BROWN 1963, GOLDSTEIN 1994, HEIMPEL and BOER 2008). Although, occasionally males produced mitotically from maternal genes, and the parental sperm cell involved to transfer an identical band of maternal chromosomes to the offspring (HAIG, 1993, KUIJPER and PEN 2010). Therefore, haplodiploid sons do not carry genes from their fathers (FILIA et al. 2015). The female offspring produced from such a sex-determination system is more advantageous. Because their mother developed through meiosis, cell division processes and carries both the paternal and maternal chromosomes known as diploid.

The genome size in the order Thysanoptera was first estimated in *Franklinothrips orizabensis (*Johansen) (Thysanoptera: Aeolothripidae), *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), *Frankliniella fusca* (Hinds) (Thysanoptera: Thripidae), and *T. tabaci*. The ploidy level of males and females for *F. orizabensis*, *F. occidentalis*, and *F. fusca* were consistent as haploid males and diploid females. However, the diploid male has not been reported in the order Thysanoptera until now except *T. tabaci* (JACOBSON et al. 2016 and 2013). This indicates that the ploidy level in *T. tabaci* is not absolute and should not be considered fixed ploidy level or should be considered due to genetic disorder. The diploid males in the thelytokous female are coherent with the tetraploidy females, indicating that the reduction of maternal genome size in a tetraploid female would produce a diploid male. Arrhenotoky can exist without haplodiploidy in a case if a homozygous individual develops to diploid through the fusion of the first two haploid cleavage nuclei. One of the haploid genomes subsequently develops with tightly packed and generally unexpressed DNA. This process is described as diploid arrhenotoky and occurs in some scale insects (NUR 1972).

3.2.3. Thelytoky

The thelytokous reproductive mode is a type of parthenogenetic asexual reproductive mode. In this reproductive mode, females transmit only maternal genes clonally and produce only daughters. Either genetically inherited or intracellular bacteria determine the thelytokous reproductive mode commonly found in many arthropods species (DOUGLAS 1998, DE VRIES et al. 2008, NEWTON et al. 2016). The endosymbiotic organisms reproduce within the generative cells (sperm and ovaries) of the host, persist mutually for a prolonged time, and favoured to manipulate the reproductive biology of their hosts (WEINERTM et al. 2015).

Endosymbiotic bacteria manipulate thelytokous reproductive mode for three purposes, such as (1) to induce the changes in reproductive modes of the host (ENGELSTA and TELSCHOW 2009, WEEKS et al. 2003, KAGEYAMA et al. 2012); (2) to improve the survival rate and evolution of the hosts (MORAN and TELANG 1998); (3) to enhance their own transmission and reduce the gene flow between populations (ENGELSTA and TELSCHOW 2009). In spider mites, the prevalence of endosymbiotic bacteria is significantly more common in females than males, suggesting it might be behaving as a sex-ratio distorter (DURON et al. 2008). *Wolbachia*, *Cardinium*, *Rickettsia* and *Spiroplasma* are the most commonly studied insect reproductive manipulators. Wolbachia was detected in *Aptinothrips rufus* (Haliday) (Thysanoptera: Thripidae), *Caliothrips fasciatus* (Pergande) (Thysanoptera: Thripidae), *Echinothrips americanus* (Morgan) (Thysanoptera: Thripidae), *Franklinothrips vespiformis* (Crawford) (Thysanoptera: Aeolothripidae), *Gynaikothrips ficorum* (Marchal) (Thysanoptera: Phlaeothripidae), *Heliothrips haemorrhoidalis* (Bouche) (Thysanoptera: Thripidae), *Hercinothrips femoralis* (Reuter) (Thysanoptera: Thripidae), *Parthenothrips dracaenae* (Heeger) (Thysanoptera: Thripidae), *Suocerathrips linguis* (Mound and Marulo) (Thysanoptera: Phlaeothripidae), *Sciothrips cardamom* (Ramakrishna) (Thysanoptera: Thripidae), *Thrips palmi* (Karny) (Thysanoptera: Thripidae) (ARAKAKI et al. 2001, KOIVISTO and BRAIG 2003, KUMM and MORITZ 2008, RUGMAN-JONES et al. 2012, JACOB et al. 2014, SAURAV et al. 2016, VAN DER KOOI and SCHWANDER 2014). However, endosymbiotic organisms are not involved in the thelytokous *T. tabaci* lineage (NAULT et al 2006).

The major features of thelytoky reproduction biology are: (a) reproductive efficiency, (b) there is no energy wastage for mating and (c) a lack of recombination between the genomes of different individuals. Genetic variability has been reported among populations within the thelytokous lineage. For example, the thelytokous *T. tabaci* strain comprises a diploid and tetraploid genome (JACOBSON et al. 2013 and 2016). The polyploidy genome might be favouring the thelytokous reproductive mode (NGUYEN et al. 2015). There are two major cytoplasmic

mechanisms to induce the thelytokous parthenogenesis and both resulting diploid individuals, such as automictic and apomictic thelytoky.

Automictic thelytoky: It follows a meiosis cell division process where a new progeny obtained from a product of a single meiotically dividing cell, crossing over during meiosis retained. The diploid eggs formed by the fusion of sister or non-sister nuclei containing recombinant chromosomes (MOGIE 1986, HEIMPEL and BOER 2008). Gamete duplication goes homozygous after one generation. Likely, recombination does not have any impression on the form of the distribution of the numbers of deleterious mutations per individual (HACCOU and SCHNEIDER 2003), diploidy is regenerated during or after meiosis and chromosome number may be doubled during the first mitotic division following meiosis and giving rise to diploid eggs that are homozygous at all loci (ENGELSTA 2008). Mostly automictic thelytoky is common in Hymenoptera insects and the diploid female is obtained by terminal fusion, central fusion and gamete duplication (STENBERG and SAURA 2009, RABELING and KRONAUER 2013,). Although, thelytoky occurs in the thelytokous females of *T. tabaci* lineage (JACOBSON et al. 2016).

Apomictic thelytoky: It follows a mitotic cell division process; thus, it does not require full meiosis cell division and fusion of meiotic cell products. The eggs are formed through complete suppression of meiosis and the progenies consist of the identical genome to their maternal (ENGELSTA 2008, RABELING and KRONAUER 2013). Solely one cell division mastered during the mitosis process and the number of chromosomes has not reduced. The diploid females obtained from the true clones of the mother due to the lack of genetic recombination. Over time, mutations are thought to accumulate independently in the two alleles at any given locus, leading to genetic divergence and high levels of heterozygosity in ancient apomictic lineages. However, meiotic recombination in apomictic lineages can lead to the loss of heterozygosity, which can have a stronger effect on genome evolution than the accumulation of mutations. It is common in aphids, the beetle Micromalthus, Cecidomyid midges and Cynipid wasps (STENBERG and SAURA 2009). Even though it has not been reported in thrips species, it can not be out of it since the thelytokous reproductive mode is a common phenomenon in *T. tabaci*.

3.2.4. Deuterotoky

Deuterotoky occurs when unfertilized eggs develop into either males or females. Deuterotoky is an uncommon parthenogenetic mode of reproduction in thrips and was reported for the first time occurring in *T. tabaci* by NAULT et al. (2006). There are some suspected reasons that such mode of reproduction is due to some external factors such as pupal insemination. The

second factor might include the mating between mother and son resulting in inbreeding depression that caused reproductive irregularity by increasing the homogeneity and decreasing heterogeneity of individual genome. Such external factors might lead to wrong conclusions regarding deuterotokous mode of reproduction.

3.2.5. Pupal insemination

The reproductive organ of the pupa develops prematurely; for this reason, immediate egg fertili-zation is not common. However, a most unusual form of coupling has been reported in *Limothrips denticornis* (Haliday) (Thysanoptera: Thripidae) in which a mature male mated with female pre-pupa (LEWIS 1973). The adult males of *F. occidentalis* were able to mate with the last stages of female (OGADA et al. 2015 not published). Insect's reproductive organs comprise a spermatheca that are used to store male sperm during hibernation and to fertilize the eggs laid next spring (LEWIS 1973). In some cases, although the adult male mated with the immature female, the male sperm might be stored in the immature female spermatheca. Thus, later on, when this female became an adult, this male sperm could be used to fertilize the eggs, and thus, an already mated female during the immature stage will be producing a combination of male and female progenies which leads to report wrong conclusion despites of deuterotokous reproduction mode.

3.3. Sex ratio

Species with haplodiploid reproductive mode often have a female-biased sex ratio (LIU and SMITH 2000). Both females and males occurred on tobacco (*Nicotiana tabacum*), potato (*Solanum tuberosum*) and onion (*Allium cepa*), as well as on weed plants as *Galinsoga parviflora*, *Datura stramonium*, *Stellaria media*, and only females occurred on cabbage (JENSER et al. 2006). The populations of *T. tabaci* are most often female-biased (LEWIS 1973). However, the ratio of males and females is frequently varied on the different host plants, regions, latitudes and seasons (KENDALL and CAPINERA 1990, JENSER et al. 2006,).

The sex ratio variation may be due to low heterozygosity (GRAUR 1985), degrees of inbreeding (HARDY 1994), quality of host plants (CHARNOV 1982) and dispersal nature (KRANZ et al. 2000). HAMILTON (1967) stated that sex ratio bias occurs due to local mate competition. It would explain the fact that females mating statues before dispersing will affect the sex ratio. For example, when the virgin female dispersed to new habitats will have male progeny, and when mated female dispersed to new habitat will have female biased progeny. The variation in sex ratio may occur due to temperature variation most likely, at warmer season fewer male than female (LEWIS 1973).

The occurrence of males and females within its geographical distribution is different even though both have the same host plant. Example on onion plants the proportion of male and female in Colorado (1♂6♀♀) (KENDALL and CAPINERA 1990), in Iowa (1♂ 10 ♀♀) (HARRIS et al. 1936), Michigan (1 ♂ 113 ♀♀) (SHULL 1914), Sudan (1 ♂ 300 ♀♀) (McGill, 1927 cit. LEWIS 1973), on garlic, leek, onion in Central Spain (1 ♂ 2♀♀) (TORRES VILA et al. 1994), Netherlands (1 ♂ 25 ♀♀) (VIERBERGEN and ESTER 2000).

In Hungary, only the thelytokous populations of *T. tabaci* lineage is an important pest of white cabbage (FAIL and PÉNZES 2004). Later, according to the investigations carried out on a potato field, the ratio of males in the population continuously changed in the vegetation period. The proportion of males was highest in June until the beginning of July and was subsequently decreasing in summer becoming the lowest at the end of August (JENSER et al. 2006).

There seems to be geographical variation in the presence of males in different populations of the same species. *T. tabaci* is cosmopolitan, but males are absent or rare throughout much of its geographical range. Example no males were observed in Italy (MARULLO 2004), in France (Bonnemaison, 1939 cit. JENSER et al. 2006), in India (Bonnemaison, 1939, cit. JENSER et al. 2006), in Java (FRANSSEN 1932), in Taiwan (TAKAHASHI 1935), in Japan (SAKIMURA 1937), in New South (NORRIS 1951) and Illinois (USA) (STANNARD 1968). Large numbers of *T. tabaci* males have only been collected in the eastern Mediterranean where its primary host, *Allium*, is native (MOUND 1992). KENDALL and CAPINERA (1990) have reported that the worldwide distribution of the proportion of males is highly correlated with longitude and the majority of arrhenotokous populations occur in the western hemisphere.

Insect species adjust the sex of their offspring by manipulating the access of sperm to the egg (WERREN 1987). Time until mating may also affect the sex ratio. In *Aphelinus asychis*, females mated later in life produced a more female-biased sex ratio (around 60 %) after mating than females mated at emergence (40-50 % females) (FAUVERGUE et al. 1998). This indicated that females enabled to adjust the progeny sex ratio by manipulating the proportion of inseminated eggs they lay, and therefore, progeny sex ratio is a function of the time that their mother spends as a virgin.

Thysanoptera species are unable to control their flight patterns and are effectively aerial plankton, except at local scales (LEWIS 1973, SMITH et al. 2015). Long fringed wings that are normally held tight against the body along the dorsal line are extended and beaten, allowing the thrips to lift off from the plant surface. Although it produces widespread scattering. Consequently, high levels of virginity in thrips population are not unexpected due to the lack of mate contact after dispersal (KRANZ et al. 2000). The sex ratio of thrips depends on environmental conditions (e.g.

temperature) (BRODSGAARD 1994, GAUM et al. 1994, RIJN-VAN et al. 1995, TSAI et al. 1995). The ratio of *Elaphrothrips tuberculatus* varies from almost 1:1 to strongly females biased throughout the year dependent on seasonal variation (CRESPI 1988a).

3.4. Sex identifications

Sexual dimorphisms are more obvious in the onion thrips and can be identified by the naked eye, but examination with a magnifying glass or microscope is usually necessary. Males of onion thrips are always smaller and, usually paler in colour than females, and known by its elongated parallel-sided and thin abdomen bluntly rounded at the tip. Females have a saw-like ovipositor, which usually lies retracted beneath a gradually tapered abdomen or conical tip of the abdomen. Identification of male and female would be possible at pupal and adult stages (LEWIS 1973). Female at the pupal stage is distinguished from the male by their larger and wider abdomen. However, it is difficult to distinguish females from males at the prepupal stage. Although, the reliable method to distinguish male and female is at first and second instar larval stages using a magnified microscope (VIERBERGEN et al. 2010).

3.5 Mating behaviour

Mating of thrips is the transfer of male sperm to the female spermatheca. Mating occurs immediately when the female becomes adulthood. For example, the pre-mating time in arrhenotokous *T. tabaci* lineage is 260 secs (LI et al. 2015). Mating occurs when a male climb on the back of the female facing the same direction and twists its abdomen sideways under the end of the female abdomen. A single male can mate with many females. A single or few matings may provide females with sufficient male sperm to reach their reproductive potential. *T. tabaci* female's mate multiple times during their lifetime. However, there are some thrips species that mating occurs only one time or remating at a very low frequency in their lifetimes such as *E. americanus* and *F. occidentalis* (KRUEGER et al. 2016, AKINYEMI and KIRK 2019).

The average mating time of Terebrantia thrips species ranges from 3 to 15 minutes and some Thripidae copulate for a long time, example *A. apteris* copulated more than 60 minutes with an average of 35 minutes (STRAUSS and KARBAN 1995). The mating duration of *T. tabaci* is about 183 secs (LI et al. 2015), In *F. occidentalis* successful copulation ranges from 114 to 595 secs with an average of 240 sec (TERRY and SCHNEIDER 1993). Females that mated for less than 69 seconds produced only male progeny, proposing that no insemination occurred during shorter mating times. Copulation interest of thrips varied with different temperatures, for example, in *C. fasciatus* the mating is much quicker when the temperature exceeds 35 °C (LEWIS 1973).

3.6. Inbreeding depression

Inbreeding is the mating between relatives that carry an identical allele (MORITZ 1986). Mating between relatives occurs in a small insect population because the access to mate with unrelated individuals is limited. In a higher population density, inbreeding might not be expressed due to unlimited access to mate with unrelated species. Inbreeding decreased heterozygosity and enforced to reduce the reproductive fitness of the next generation. The harmful consequences of inbred matings referred to as inbreeding depression (HEDRICK and GARCIA-DORADO 2016). Repeated full relative mating leads to a decline in population size (WRIGHT et al. 2008). Inbreeding depression is much more dangerous in a small population in a case when the related individual mate each other for subsequent generations. Frequent mating between relatives causes to increase in the accumulation of deleterious mutation (LANDE 1995, WOODWORTH et al. 2002) and is a major cause component of extinction vortices that threaten small populations (SACCHERI et al. 1998, FRANKHAM 2005).

Inbreeding favours homozygosity in the genome and allows similar recessive deleterious alleles, which induce the reproductive fitness reduction of the progeny such as fecundity, egg hatchability, immature survival, and adult longevity (SACCHERI et al. 1998). Inbreeding depression is more intense in diploid species than in haplodiploid species (HEDRICK and PARKER 1997, HENTER 2003). The variation in reproductive fitness is due to the level of selection of recessive deleterious alleles. Subsequent counter selection of deleterious recessive alleles in haploid males significantly reduces the genetic load and due to this, haplodiploid species carry fewer recessive deleterious alleles than diploid species (ROFF 2002CHARLES, WORTH and WILLIS 2009). Because the haploid male imposes purifying selection of recessive deleterious alleles and hence exposed to continuous selection which greatly decreases their frequency in the population (AVERY 1984, WERREN 1993). However, alleles of genes only expressed in the diploid females are protected against purifying selection in heterozygous individuals. In haplodiploid, the genetic load that is hidden in heterozygous female diploids should be expressed and thus purged in the haploid males. This leads to the prediction that haplodiploids suffer more from inbreeding effects on life-history traits (SAITO et al. 2000). The effect of inbreeding has been studied in Coleoptera, Hymenoptera, and Lepidoptera insect species and in the plant species. However, the effect of inbreeding in the Thysanoptera insect species has been not studied. As *T. tabaci* is belonging to haplodiploid insect pest species, mating between brother and sister, and mother and son may be the main factor that induced the effect on the fecundity, egg hatchability rate, adult longevity and the sex ratio of the progeny.

3.7. Oviposition behaviour

The two-suborder Thysanoptera thrips species distinguished in their oviposition behaviour and the morphological attributes of these two suborders. Terebrantian females have a well-developed ovipositor consisting of a basal apparatus and a shaft. The ovipositor is downwards in Terebrantia and curved upwards in Aeolothripidae (HEMING 1970, MORITZ 1997). The ovipositor of Terebrantia is used to pierce plant tissue and deposit the egg, whereas Tubuliferan ovipositors are reduced to a U-shaped chute (HEMING 1995) and eggs are laid on the surface of the substrate (LEWIS 1973). Terebrantian lay eggs singly into plant tissue but Tubulifera may lay clusters of eggs at oviposition sites that in some species are guarded by males or females. *S. linguis* the females lay eggs in different places on the plant but then transport them by pushing the eggs with their legs to a single batch.

3.8. Male fighting behaviour

Fighting occurs between males of many insect species when competing for food (BLANCKENHORN 1991), mating (WEST et al. 2001), oviposition site (MOORE AND GREEFF 2003), keeping territory (KEMP and ALCOCK 2003) and egg guarding (CRESPI 1992). Fighting between two opponent's results in either victory or loss (CHASE et al. 1994). The winner often dominates the competed resources. Occasionally, severe fighting leads to death in some insect species (CRESPI 1992). A number of factors determine the intensity of fighting as well as the outcome of fights between contestants such as body size and morphology (males with enlarged forelegs, tarsal claws, and large forehead win the contests), and fighting experience (MOUND 1991, TERRY and DYRESON 1996, REANEY et al. 2011;). Individual fighting performance often influenced by the outcomes of their previous contests (RUTTE et al. 2006). A competing individual with victorious experience has a chance to win the next encounter as well (RUTTE et al. 2006), and an individual with a recent history of losing is likely to lose the next encounter again and eventually leave the resources (CHASE et al. 1994). Male fighting behaviour has been observed in members of the Tubulifera suborder such as in *Hoplothrips karnyi* (Hood) (CRESPI 1988a), *Elaphrothrips tuberculatus* (Hood) (Thysanoptera: Phlaeothripidae) (CRESPI 1986a), *Hoplothrips pedicularius* (Haliday) (CRESPI 1986b), *Kladothrips rugosus* (Froggatt) (Thysanoptera: Phlaeothripidae), *Oncothrips tepperi* (Karny) (Thysanoptera: Phlaeothripidae), *Onychothrips tepperi* (Karny), *Csirothrips watsoni* (Mound), *Thaumatothrips froggatti* (Karny) and *Phallothrips houstoni* (CRESPI 1992). Fights in these thrips species are presumably associated with mating, food, and egg guarding. However, fighting is not limited to occur only in members of the Tubulifera suborder since there are a few studies reporting of male fighting behaviour in members of the Terebrantia suborder thrips species such as in *F. occidentalis* (TERRY and

GARDNER 1990, OLANIRAN and KIRK 2012) and *Frankliniella intonsa* (Trybom) (Thysanoptera: Thripidae) (KIRK 1996). *F. occidentalis* males form an aggregation in which two or more males occupy one place. During this aggregation, aggressive fighting interactions between males were observed. In insect species, mating and fighting interactions are initiated by chemical cues produced by the males such as male-specific cuticular hydrocarbons and aggregation pheromones (OLANIRAN et al. 2013).

3.9. Host ranges

Thrips tabaci has been treated as a potentially important key pest on a wide range of crop and weed species (LEWIS 1973). These polyphagous species have been recorded to occur on more than 355 plant species within 40 plant families (GHABN 1948). However, despite its large host range, it is particularly damaging to plants from the families of Brassicaceae, Liliaceae, and Solanaceae (SAKIMURA 1928, MODARRES 1997). There are a number of factors likely responsible for *T. tabaci* to use those plant families as preferable host plants. Such as due to their volatile substances, nutrition, a relative absence of predators, or plant architecture that is favourable to thrips cryptophilic and thigmotropic behaviour, and abundance of plant species during the season (LEWIS 1973).

Thrips tabaci has reported from various horticultural and ornamental plants in many places of world such as alfalfa (*Medicago sativa*), asparagus (*Asparagus officinalis*), bean (*Phaseolus vulgaris*), beet (*Beta vulgaris*), blackberry (*Rubus fruticosus*), cabbage (*Brassica oleracea*), carrot (*Daucus carota*), cauliflower (*Brassica oleracea* var. botrytis.), celery (*Apium graveolens*), cotton (*Gossypium spp*.), cucumber (*Cucumis sativus*), garlic (*Allium sativum*), kale (*Brassica alboglabra*. Bailey), leek (*Allium ampeloprasum* var. porrum), lettuce (*Lactuca sativa*), onion, (*Allium cepa)*, parsley (*Petroselinum crispum*), pea (*Pisum sativum*), pineapple (*Ananas comosus*), potato (*Solanum tuberosum*), pumpkin (*Cucurbita maxima*), squash (*Cucurbita spp*.), strawberry (*Fragaria ananassa*), sweet potato (*Ipomoea batatas*), turnip (*Brassica rapa* var. rapa), tomato (*Solanum lycopersicum*), grains, common burdock (*Arctium minus*), dandelion (*Taraxacum officinale*), curly dock (*Rumex crispus*), and chicory (*Cichorium intybus*) (MODARRES 1997, SHELTON et al. 2008, FEKRAT et al. 2009, SMITH et al. 2011, Gill et al. 2015, NIKOLOVA, 2018).

3.10. Economic importance

Thrips tabaci is an important key pest and reported to be the most serious pests to onion. The pest status of *T. tabaci* characterised by its polyphagous nature, high reproductive rate, short

generation time, high intrinsic rate of natural increase, cryptic habits, ability to transmit plant pathogens, and development of resistance to insecticides (MARTIN et al. 2003, SHELTON et al. 2003, 2006, MACINTYRE et al. 2005, MORISHITA 2008). This pest caused a large economic loss when they infest at a young stage of the plants (LEWIS 1973). Because at the younger stage, plants conserve more water and the damage induces more water loss (POURIAN et al. 2009). Both adults and larvae of onion thrips caused damage to its hosts in direct and indirect way.

3.10.1. Direct damage

Onion thrips has unique asymmetrical mouthparts made up of a single mandibular stylet and paired maxillary stylets. Adult and larval stages of onion thrips use the single mandible to rasp the leaf surface and pierce the epidermis. During this process, they released substances to predigest the plant tissue. Then, they siphon off the plant contents and consume mesophyll cell contents, which eventually causes a loss of chlorophyll and this interferes with the translocation of nutrients (BOATENG et al. 2014). Onion thrips damage induces whitish to silvery patches or streaks on the surface of leaves (POURIAN et al. 2009), during their feeding on leaves also create an entry point for other pathogens such as bacteria, fungus. *T. tabaci* damage to crops induces the production of ethylene which accelerates leaf senescence (KENDALL and BJOSTAD 1990). These all contributed to the reduction of onion bulb size and bulb production (NAULT and SHELTON 2008). *T. tabaci* causes 40 to 60 % foliar injury and 10 to 20 % yield losses (WAIGANJO et al. 2008). The direct feeding damage of onion thrips is estimated to cause more than U.S. $1 billion in crop losses annually worldwide (BALAN et al. 2018).

3.10.2. Indirect damage

Besides causing direct damage to its host plants, *T. tabaci* has been recognized as a vector of *Tomato Spotted Wilt Virus* (TSWV), *Iris Yellow Spot Virus* (IYSV), *Tomato Yellow Ring Virus* (TYRV) and *Alstroemeria yellow spot virus* (AYSV) (CORTÊS et al. 1998, HSU et al. 2010, MACHARIA et al. 2015, ROTENBERG et al. 2015, HASSANI-MEHRABAN et al. 2019). These tospovirus species are potentially yield devastating pathogen of onion plant and occur on other crops worldwide (GENT et al. 2004, PAPPU et al. 2009). *T. tabaci* transmitted TSWV in a persistent and cuticular manner (ULLMAN et al. 1992). Although, *F. occidentalis* has shown the ability to transmit TSWV (ALLEN and BROADBENT 1986). *T. tabaci* transmit the tospoviruses as first and second instars or adult's developmental stages (ULLMAN et al. 1992, WIJKAMP et al. 1993). The efficiency of transmission by adults decreased with age. On the other hand, the virus transmission efficiency of *T. tabaci* decreases with increasing temperature (CHATZIVASSILIOU

et al. 2002). The competence between different forms of *T. tabaci* lineages to transmit TSWV has revealed different significantly among populations, associated with reproductive biology, sex, and host plant preference (CHATZIVASSILIOU et al. 1999, 2002). The arrhenotokous tobacco-associated lineage has been known to be highly efficient in transmitting TSWV, whereas the arrhenotokous leek-associated lineage transmits TSWV inefficiently. The thelytokous leek associated lineage transmits TSWV poorly or not at all (CHATZIVASSILIOU et al. 2002, TEDESCHI et al. 2001, WIJKAMP et al. 1993). *T. tabaci* males transmitted TSWV more efficiently than females, and populations collected from tobacco transmitted better TSWV vectors than those from leek (CHATZIVASSILIOU et al. 1999 and 2002). Thelytokous individuals collected from potato transmit TSWV efficiently whereas individuals collected from Chrysanthemum failed to transmit TSWV (WESTMORE et al. 2013).

3.11. Description of life stages

As with all Terebrantia insect species in the family Thripidae, the general life cycle of *T. tabaci* consisting of an egg, two active feeding larval instars, two inactive feeding instars, and adult developmental stages (GHABN 1948, NAKAHARA 1991).

3.11.1. Eggs

Females oviposit eggs singly by saw-like structure into the leaf tissue. The saw-like structure of females used to cut the plant tissue for egg laying. Only one end of the egg is in proximity to the epidermis of the leaf tissue surface to allow the emergence of immatures. Eggs are microscopic, kidney-shaped, whitish at deposition, and change to yellow or orange as development continues, since then reddish eye spots become evident (ARRIECHE et al. 2006). On onion, the average length and width of eggs are 0.23 mm and 0.08 mm, respectively (PATEL et al. 2013). Hatching occurs in 2 to 6.5 days depending on the temperature (**Table** 3).

3.11.2. Larvae

Onion thrips larvae are similar to adult except the absence of wing and short antennae with dark colour. *T. tabaci* has two larval stages such as first and second instar larval stages. These instars have different features. The first instar larva is whitish, semitransparent and starchy which later changes to a yellowish-white colour. The second instar larva is larger in size and yellowish in colour (PATEL et al. 2013). The average body length of first and second instar larvae ranges from 0.35 to 0.65 and 0.84 to 1.14 mm, respectively (PATEL et al. 2013, SHAIKH et al. 2015). The first instar developmental time completed in about two to three days, and the second instar developmental time completed in about three to four days (POURIAN et al. 2009). The

developmental time of both first and second instar larvae can be longer in a case if there is a cooler environment. Both instars are active to feed and cause damage to crops (GILL et al. 2015).

Identification of first and second instar larvae

The first and second instars should be identified based on their size difference and morphological features. SPEYER and PARR 1941 stated that the best method to distinguish the first and second instar larvae is their number of sternal setae on the abdominal segments II-VII and the number of setae on their pro-notum.

First instars: The first instar larvae of *T. tabaci* are composed of two pairs of sternal setae on their abdominal segments II-VII, three pairs of spiracles and six pairs of setae on their pro-notum (KIRK 1987, VIERBERGEN et al. 2010).

Second instars: -They are larger and fat body size as compared to first instar larvae. This stage of *T. tabaci* family insects consists of three pairs of sternal setae on the abdominal segments II-VII, two pairs of spiracles and seven pairs of setae on the pronotum (KIRK 1987, VIERBERGEN et al. 2010).

Sex identification of onion thrips larvae

In the family Thripidae male and female gender at the first and second instar stage, have different features on their ninth abdominal segments. Such as males and females exhibit four and three pairs of setae for the first instar, respectively and five and four pairs of setae for the second instar, respectively (VIERBERGEN et al. 2010).

3.11.3. Pre-pupa and Pupa

Pre-pupa and pupa stages are inactive and non-feeding stage, and both stages found in the soil, at the base of the onion plant neck, or underneath bulb scales and in different parts of glasshouse to protect themselves against environmental effects (RUEDA and SHELTON 1995). The prepupa is whitish-yellow colour and its developmental time lasts in one to three days and its antennae are directed forward to the head. The pupa is yellowish-white, changing to yellow colour before adult emergence, and its developmental time varies from three to ten days among different geographical regions (PATEL et al. 2013).

3.11.4. Adult

Adult colour varies from pale yellow to dark brown depending on temperature and is more active as compared with larvae (SAKIMURA 1937). Adults are more mobile than the immature

stages. The forewings and hindwings are fringed and mouthparts are piercing-sucking (BHONDE et al. 2016). Winged adults are weak fliers but can fly from plant to plant or be carried long distances via wind and thus they dispersed to the main crop and initiate infestation (PAL et al. 2019). Adult females of onion thrips are about 1.1 to 1.2 mm long (PATEL et al. 2013).

3.12. Environmental factors on the occurrence of *T. tabaci*

Environmental conditions affect the presence of onion thrips. Hot and dry weather conditions cause an increase in *T. tabaci* populations and the degree of thrips injury to the onion. Because a combination of hot and dry environmental conditions causes a shorter generation time and a reduction in mortality from rain and plant pathogens. Higher temperatures shorten the developmental time, pre-oviposition period, increase the fecundity and shorten the life cycle in as long as one month or as short as two weeks (BUCKLAND et al. 2013). Heavy rain washes onion thrips from plants and causes to decrease onion thrips densities (LIU 2005).

The abundance of *T. tabaci* varies depending on the weather condition. Example, in Ethiopia, the rainy and cool season is from June to November and in these months, the abundance of onion thrips is null or significantly lower. In this country, the dry and moderate temperature is from December and during this month, the abundance of onion thrips is increased (MERENE 2015). ULLAH et al. (2010) have reported that the population density/plant increased from 3rd February to 25th February and has linearly increased during March in Pakistan. The possible reason for the increase in thrips population between February and March may be due to the temperature where it became more conducive to growth and development of the insect as well as suitable for the growth of seedlings of onions. During these months, seedlings of onion are usually larger and are more attractive to thrips. The peak population recorded in April and since then their population abruptly declined/plant during May. In New York, adults emerge from mid-May through June but do not appear to colonize onions until late June or July. Transplanted onions and early-maturing varieties are often colonized before late-maturing varieties. During the summer, onion thrips may migrate from recently cut alfalfa fields and maturing wheat fields into onion fields. In these situations, there are strong edge effects characterized by high numbers of thrips. Onion thrips migrate from maturing onions (leaves collapsed and drying) into late-maturing varieties. The sudden drop in *T. tabaci* population may be due to maturation of crop (RAUT et al. 2020).

3.13. Life history of *T. tabaci*

The complete life cycle of onion thrips is as short as 10 days when the temperature is above 25 °C and as long as more than 29 days at 15°C (**Table** 4). The life cycle of onion thrips is faster,

and slower depending on temperature, day length and available food sources (BRØDSGAARD 1994, GAUM et al. 1994, RIJN et al. 1995, TSAI et al. 1995, MURAI 2000). In cooler areas, only one or two generations are possible (LEWIS 1973, 1997).

Table 3: Lifetable parameters of onion thrips lineages on different food source

Food source	**Lineages**	**Temperature (°C)**	**Developmental time of different**					
			Egg	**L1**	**L2**	**Prepupa**	**Pupa**	**References**
n	T	27	5.11 ± 0.07	2.71 ± 0.08	3.88 ± 0.07	2.61 ± 0.05	3.68 ± 0.09	FEKRAT et al. 2009
a	L2	27	4.18±0.53	2.08±0.56	2.11±0.80	1.25±0.80	1.25±0.47	HASSANZADEH et al. 2003
c	L2	25	2.82±1.33	1.95±1.42	4.12±0.92	1.03±1.44	1.97±0.91	POURIAN et al. 2009
c	L2	25	3.92±0.32	2.13±0.45	3.17±0.45	1.09±0.23	2.43±0.23	VAN RIJN et al. 1995
a	L2	20	6.7±0.04	3.2±0.05	5.5±0.15	1.9±0.05	3.8±0.06	LI et al. 2014
b		20	6.5±0.53	2.8±0.40	3.6±0.06	1.5±0.02	3.5±0.02	
a	L1	20	6.6±0.03	2.9±0.04	4.4±0.09	1.6±0.03	3.6±0.03	LI et al. 2014
b		20	6.5±0.47	2.9±0.45	3.7±0.10	1.6±0.02	3.4±0.03	
a	L2	24	3.6	6.4		1.2	3.2	SAKIMURA 1937
		18.8	5.6	8.6		2.0	4.2	
		15.5	6.5	13.5		2.8	6.3	

Where, h= honey and pollen, a= *Allium cepa*, c= *Cucumis sativus*, b= *Brassica oleracea*, n= *Nicotiana tabacum*

Table 4: The total fecundity, lifespan and pre-oviposition period of *T. tabaci* adult stages on different food sources

Food	Lineages	Temp. (°C)	Total fecundity	Preoviposition (Days)	Lifespan (days)	References
n	T	27	26.35±1.93	2.50±0.25	19.07±1.51	FEKRAT et al. 2009
a	L2	18	80.1	2.8	58.2	SAKIMURA 1937
a	L2	15	53.9	3.9	51.7	
a	L2	14	-	8.8	-	
c	L2	25	-	1.9±0.26	-	VAN RIJN et al. 1995
h	L2	30	62.6±34.9	1.96±0.64	12.8±4.6	MURAI 2000
		25	165.0±84.8	2.35±0.56	25.0±10.2	
		23	270.4±111.6	3.41±0.71	41.7±14.5	
		20	210.0±148.9	4.37±0.56	46.8±21.4	
		15	169.6±94.2	8.64±0.65	86.6±36.6	
a	L2	27	31.63±18.86	3.60±1.28	16.15±7.58	HASSANZADEH et al. 2003
a	L1	25	29.50 ± 2.24	2.35 ± 0.16	18.00 ± 1.03	FEKRAT et al. 2009
c	L2	25	26.82±5.56	2.0	18-21	POURIAN et al. 2009
a	L2	20	84.9±10.0		28.7±2.4	LI et al. 2014
b		20	113.6±8.4		35.7±2.2	
a	L1	20	118.7±11.0		29,8±1,9	LI et al. 2014
b		20	84.9±6.1		38.3±3.0	

Where, h= honey and pollen, a= *Allium cepa*, c= *Cucumis sativus*, b= *Brassica oleracea*. n= *Nicotiana tabacum*

3.14. Overwintering of *T. tabaci*

Adults of onion thrips overwintered during harsh environmental conditions (NORTH and SHELTON 1986, CHO et al. 1995, JENSER et al. 2003, LARENTZAKi et al. 2007). Knowledge of the overwintering ecology of onion thrips is useful for predicting the abundance and dispersal of this pest in an onion ecosystem. Sites for overwintering include soil within and adjacent to onion fields, on onion culls, in vegetation near onion fields, and in other crops such as alfalfa, wheat, and clover (LARENTZAKI et al. 2007). Although, *T. tabaci* can also overwinter in volunteer onion plant parts, leaf litters field edges. Volunteer onion plant parts are bulbs that were unknowingly left in the field at harvest (CHO et al. 1995). These volunteers will survive in winter and they will sprout in spring and will be accessible and ready for use to onion thrips long before commercial onion crops are attractive. They may also overwinter within the crop in the sheltered microclimate provided by plastic and straw mulches.

Diapause is one way of adaptation that is used to prevent their reproduction (DANKS, 2004). Temperature and photoperiod are the two environmental cues that affect lifetable parameters and reproductive diapause of insect species (KAMM 1972, LEWIS 1973, BRODSGAARD 1994; EKESI et al. 1999, PULLIN 1986). The diapause effect occurs at egg, larval, pre-pupal, pupal or adult developmental stages (MURAI 1987). During unfavourable environmental conditions, insects become dormant and adjust their physiological and behavioural activities. Insects living at higher latitudes subsequently show overwintering diapause when the autumn night length falls short of a critical value (SAUNDERS 2002).

3.15. Monitoring and treatment decisions to *T. tabaci*

Early identification of a pest's species is an important component to designing IPM strategies. Onion thrips emerge from overwintering sites and colonize weeds and any other volunteer plants (GILL et al. 2015). Thus, an infestation usually begins from field edges than other parts of the farm. Therefore, samples might be taken randomly from different parts of the field most, likely from the field edge and middle part of the field (LARENTZAKI et al. 2007). Field and laboratory-based sampling methods used to evaluate the infestation of onion thrips in the farm fields.

3.15.1. Field sampling

Onion thrips highly invade the onion field margins at the early and mid-spring seasons and then disseminate to the inside parts of onion farms, so, at the beginning of the spring, samplings should be taken from boarder plants. As onion thrips prefer the younger stages of the plant, the

primary samplings should be taken from the young onion plants in the lowest center part of the leaf sheath (SHELTON et al. 1987).

3.15.2. Laboratory-based sampling method

The infestation of onion fields with thrips should be evaluated using sticky boards, glue-based traps made of high-quality polypropylene material. For thrips species blue colour is reliably effective traps (JASROTIA et al. 2016). Fluorescent yellow traps were the most effective traps while blue traps were the least attractive for monitoring *T. tabaci* both in the field and in the greenhouse (RŐTH et al. 2016). On the other hand, blue traps were the most attractive to *T. tabaci* followed by yellow and white ones (POBOZNIAK et al. 2020).

Odour baits and olfactory response: Chemical attractants are spread in sticky cards with the function of luring thrips (MUVEA et al. 2014). They are commercially available (ABDULLAH et al. 2015). A variation consists of volatile compounds mixed with water and placed in plastic containers (0.5 L) suspended on wooden stakes (RIESKE and RAFFA 2003).

Leds in sticky traps: Evaluated by CHEN et al. (2004) as a monitoring method for western fower thrips. Light-emitting diodes (LEDs) are attached to sticky cards. Caged sticky cards are covered with a nylon mesh screen to prevent the capture of large insects, which might saturate the sticky cards and prevent the capture of thrips (CHEN et al. 2004). Management decisions are made based on the plant colonization threshold.

Ground traps, pupation papers, or carton trap: Sticky traps are placed under plants to collect pupating larvae that drop off plants to pupate in the soil (TANIGOSHI and MORENO 1981; RHODES and MORSE 1989). A variation consists of folded papers that are distributed among horizontal twigs, above the ground, or inside the plant canopy; it captures immature thrips (RHODES and MORSE 1989).

Generally agree that more thrips are attracted by low-UV-reflective white, blue and yellow surfaces than by green, red, black and highly-UV-reflective white ones. Thus, both colours might be effective trapping for *Thrips tabaci*. However, since, there are a different research reports on the effectiveness of different colour traps by different authors, the differences was probably due to the UV light reflectance, the types of glue. UV light reflectance has been reported in the L1 and L2 lineages, and both lineages are able to detect UV light. (EGRI et al. 2020). Thus, UV light is an important spectral component that must be taken in to consideration for L1 and L2 *T. tabaci*lineages when designing colour traps.

3.15.3. Action threshold

It is one of the most important decision-making elements in IPM. The reliable treatment threshold level for *T. tabaci* varies based on season (dry or rainy), geographical region, and the resistance level of crop cultivars used, and environmental conditions. For example, the following threshold levels were suggested: in California 30 thrips per plant (EDELSON et al. 1989), in New York state 3 individuals per leaf (NAULT and SHELTON 2012), in Ethiopia 5-10 thrips per plant (SHIBERU and MAHAMMED 2014), and in Honduras 0.5-1.6 individuals per leaf in the dry season (RUEDA et al. 2007).

3.16. Management tactics

The risk of large economic losses due to the infestation of greenhouse and field crops by *T. tabaci* requires the use of control measures (DIAZ-MONTANO et al. 2011). Onion thrips has been controlled by the use of foliar insecticides. However, due to their cryptic nature, high reproductive capacity, multi-generations per year, hidden lifestyle (pupation in the soil), resistance to several pesticides, and polyphagous nature makes them hard to control by synthetic insecticides. In addition, the eggs laid into the leaf tissues where it may escape control. Re-infestation of fields can occur from surrounding non-crop vegetation and immigration of thrips from nearby fields. In addition, some *T. tabac* biotypes are resistant to insecticides in different parts of the world (FOSTER et al. 2010, NAULT and SHELTON 2012). The reliable and accurate prevention of onion thrips needs to be integrating with diverse management tactics to influence onion thrips populations in different interacting ways.

3.16.1. Host plant resistance

Host plant resistance provides long-term prevention of onion thrips (KENNEDY 2008). Resistance cultivars are important to reduce the use of insecticides and delay the development of insecticide resistance. Reducing the number and frequency of insecticide application enhances the natural enemy of onion thrips (BIANCHI et al. 2006). DIAZ-MONTANO et al. (2012) has reported that OLYS05N5, Tioga, Peso, Calibra, Vaquero, Cometa, Medeo, NMSU 03-52-1, Delgado, T-433, Colorado 6, Arcero, Mesquite, White Wing, and Granero. Some resistant onion cultivars develop specialized morphological structures that make them less attractive to onion thrips, such as yellow-green, glossy to semi-glossy leaf surfaces, waxy leaves, and tight necks. The resistance level of the onion cultivar is correlated with the glossy and semi-glossy levels of epicuticular waxes (DAMON et al. 2014). Therefore, onion cultivars with low epicuticular waxes are more resistant to onion thrips.

3.16.2. Cultural control

Destroying *T. tabaci* overwintering sites such as cull onions, volunteer onion plants, weed hosts and sanitation of the farm edges are necessary to control the population of this pest (LARENTZAKI et al. 2007). In small-scale onions, farm overhead irrigation of onion crops can wash thrips and cause dramatic population reductions. Mixed cropping carrots with onions reduced the densities of *T. tabaci*. Because, diversified plant habitat acts as a major food host of the pests, or may hide the target crop from thrips view (UVAH and COAKER 1984). On the other hand, the enhancement of plant diversity acts as reserviours of natural enemies that have the potential to control thrips (DENYS and TSCHARNTKE 2002). The population of *T. tabaci* suppressed by mulching. Because mulches reduce weeds, conserving soil moisture, increase soil temperature and reduce soil erosion and some mulches repel insects (GILL et al. 2011, GILL and MCSORLEY 2012, GILL and GOYAL 2014).

3.16.3. Insecticides

Synthetic insecticides have been commonly used against onion thrips. The effectiveness of these chemicals is varied based on the threshold levels of onion thrips (MACINTYRE et al. 2005). For example, spinetoram effectively managed onion thrips when it applied after three larvae per leaf but at this threshold level lambda-cyhalothrin, methomyl or formetanate hydrochloride are not effective SHELTON et al. 2003. However, *T. tabaci* infestations were managed by methomyl and formetanate hydrochloride when the threshold level of one larva per leaf threshold (NAULT and SHELTON 2010). The efficiency of insecticides decreased as the *T. tabaci* populations reached more than five larvae per plant. Repeated application of chemical insecticides in the field and greenhouse often favours unwanted effects such as pesticide resistance, elimination of non-target species (like pollinators, natural enemies, and detritivore organisms), pest resurgence, and secondary pest outbreaks (FOSTER et al. 2010).

3.16.4. Aromatic plants

There have been trials to establish aromatic insecticides from various plant species to control onion thrips at field and greenhouse conditions and the following have been recommended: *Artemisia arborescens, Azadirachta indica L., Chrysanthemum cinerariaefolium, Datura stramonium, Dodonae angustifolia L., Dianthus caryophyllus*, *Melaleuca alternifolia, Nicotiana glauca, Origanum* majorana, *Ocimum gratissimum, Rosmarinus officinalis*, *Tagetes minuta* (TOL et al. 2007, PRABHU et al. 2011, SHIBERU and NEGERI 2014, FITIWY et al. 2015). In Ethiopia *Nicotiana spp., Phytolacca dodecandra*, *Securidaca longepedunculata, Nicotiana tabacum* were effective against onion thrips under field condition (SHIBERU et al. 2013).

Aromatic plants are used as spraying in field and greenhouse conditions and applied according to procedures similar to those used to chemical insecticides (STEPANYCHEVA et al. 2019). The essential oils diluted in water or formulated products are sprayed before planting or later on foliar. A recent study reported that pulverized neem plants have systemic action when sprayed onto the soil and thus roots absorb it and translocate within the body. Sometimes aromatic insecticides can be effective in the form of fumigation in the greenhouse (KOSCHIER 2008).

However, the effectiveness of some aromatic plant products may be not enough for high density of onion thrips. The reason for the ineffectivness of their controlling may be due to short residual property of the prepared plant parts and their rapid oil volatility that make them less toxic to the targeted pests. For this matter, with a practical point of view, aromatic plants may be more effective when they are mixed with other control methods. It is recommended that weekly repeated applications at least three times until harvest should be necessary to decrease the density of onion thrips below the economic injury level. Aromatic plants are much more effective in a condition where the population of onion thrips is lower or moderate (NAULT and SHELTON 2012).

Plant-based bioactive compounds offer a variety of biological mode of actions against onion thrips acting as attractants, repellents, antifeedants, anti-ovipositional agents, poisoners, fecundity reducers, perpetrators of egg sterility, and metamorphosis inhibitors (KOSCHIER et al. 2001, KOSCHIER and SEDY 2003, STELLA et al. 2010, SANIEWSKI et al. 2014).

Attractant activity: Onion thrips is a small insect and lives in the curled leaves, which leads to omitting it easily during monitoring. This problem can be solved by placing coloured sticky boards traps (VERNON and GILLESPIE 1990). Trap effectiveness could be increased by combining an attractive colour cue with an attractive odour cue (TEULON et al. 2007). An attractive odour derived from aromatic plants is a complex mixture of different secondary metabolites such as monoterpenes, sesquiterpenes, and phenylpropanoid compounds. Combining two or more attractive secondary metabolites to increase their effectiveness could seem a common practice toward trap efficiency improvement. However, the mixing of p-anisaldehyde and methyl isonicotinate had less efficiency for onion thrips compared to applying them separately (TEULON et al. 2007). This implies that onion thrips would have only one odor receptor, therefore blended compounds could mask each other (NOTTINGHAM et al. 1991, KOSCHIER 2008).

Repellent activity: Plants produce odours that often are repellents to numerous species of insects. Therefore, colonization is preceded with testing various plant cues such as colour, shape, and size of the plants (LEWIS 1973). Repellents are products of secondary metabolites, used as olfactory messengers to interfere, and dis-courage insects from landing or movement onto plant surfaces. In New Zealand, onion thrips was repelled by *Rosmarinus officinalis* essential oil and

deterred by *Dodonae angustifolia, Ocimum gratissimum,* Origanum majorana essential oils and the controlling efficiency against onion thrips was about 71-87% (TOL et al. 2007).

Oviposition deterrent: The interaction of the plant and pest is not limited to feeding but also interferes with egg deposition. Plant nutritional quality, particularly nitrogen content, architecture, morphology, anatomy, and secondary compounds have been reported as detrimental factors for ovipositional choice of *T. tabaci* females (KOSCHIER and SEDY 2003, SINGH and SARATCHANDRA 2005). A field study with *Azadirachata indica* extracts showed that the action against onion thrips was correlated with nutritional deterrence and discouraging egg lay, as well as with toxicity and infertility. The physiological toxicity of azadirachtin is based on growth retardation, which reduces the female fecundity, and thus reduces the density of *T. tabaci* on onion (SHIBERU and NEGERI 2014).

3.16. 5. Biological control

Entomopathogenic fungi

Some fungi species effecient to kill insects by their colonization. *Beauveria bassiana, Metarhizium anisopliae, Lecanicillium (Verticillium) lecanii/ muscarium, Entomophthora parvispora, Entomophthora thripidum, Paecilomyces lilacinus, Neozygites parvispora* have been tested against onion thrips (CARL 1975, MACLEOD et al. 1976, SAMSON et al, 1979, MANIANIA et al. 2003, ABE and IKEGAMI 2005, THUNGRABEAB et al. 2006, EZZATI-TABRIZI et al. 2009, ANNAMALAI et al. 2013, WU et al. 2016). According to THUNGRABEAB et al. (2006), about 36 isolated entomopathogenic fungi species effectively lowered the onion thrips population; however, the pathogenic efficiency varied among the species. In another report, *B. bassiana* significantly lowered the population of larval and adult stages of onion thrips under greenhouse conditions (WU et al. 2013). A report in western Kenya revealled that the entomogenous fungus *M. anisopliae*, has the potential to control thrips in onion (MANIANIA et al. 2003). In Ethiopia, *B. bassiana* significantly decreased onion thrips density at field condition (SHIBERU and NEGERI 2014).

The mode of actions of these entomopathogenic fungi is associated with their contact with the host insects. These fungal species often need wet conditions to allow the filamentous growth and production of conidia. The infection processes involve: 1. attachment of the spore to the host's cuticle; 2. germination of hyphae on cuticle that produce enzymes, such as proteases, chitinases, quitobiases, upases, and lipoxygenases, which penetrate the host's cuticles and epidermis, degrading the insect's cuticle that facilitates the process of penetration; 3. once hyphae entered to inside of the host's body they disseminate through the hemocele and invade different tissues, fatty

bodies, Malpighian tubules, mitochondria, and hemocytes, leading to death of the insect within 3-14 days after infection. Once the insect dies and many of the nutrients are exhausted, fungi start micellar growth and invade all the organs of the host. Finally, hyphae penetrate the cuticle from the interior of the insect and emerge at the surface, where they initiate spore formation under appropriate environmental conditions (SENTHIL-NATHAN 2015).

Entomopathogenic nematodes

Nematodes are present in the soil, cover crops and affect insects upon contacts (CHAŁAŃSKA and ŁABANOWSKI 2014). Steinernema and Heterorhabditis are the two most studied nematode genera that were suggested as biocontrol agents against insects. The most effective nematode species against onion thrips are *Steinernema feltiae*, *Steinernema carpocapsae*, *Heterorhabditis bacteriophora*, *Heterorhabditis indica* (MOLYNEUX 1982, BEDDING and KASHKOULI et al. 2014, AZAZY et al. 2018). Usually entomopathogenic nematodes are effective when they are applied to moist soil and in the evening or early morning. Post- irrigation application increases the effectiveness of nematode establishment and washes the nematodes from the leaves into the soil, which is used as a natural reservoir (SIMÕES and ROSA 1996). In Netherland, Great Britain and Germany, the use of entomopathogenic nematodes in the field is approved either solely or in a mixture utilizing common spray equipment (JUNG 2004). In Egypt, foliar spraying of *H. bacteriophora* and *H. indica* with adequate concentrations was successful in lowering the onion thrips populations at field conditions (AZAZY et al. 2018). These entomopathogenic nematodes were more effective on nymphal stages than adults. *S. carpocapsae*, *S. feltiae* and *H. bacteriophora* were tested against onion thrips in the laboratory and were more effective on prepupa and pupa stages (KASHKOULI et al. 2014).

The modes of actions of the entomopathogenic nematodes are: 1. infective juvenile nematodes migrate and search new hosts and colonize them entering the hosts' body through mouth, anus, and spiracle; 2. these nematodes release *Xenorhabdus* bacteria to kill the host; 3. the parasites Heterorhabditidae and Steinernematidae transform into adults in the dead hosts' body; 4. adult females and males of these nematodes reproduce in the dead hosts; 5. eggs of the parasites pass through different developmental stages and the third juvenile stage again begins to search the new hosts (GREWAL and GEORGIS 1999, SENTHIL-NATHAN 2015).

Predators

The effective predators that predate onion thrips are *Amblyseius barkeri, Amblyseius cucumeris, Amblyseius swirskii, Chrysopa carnea, Chrysopa vulgaris, Deraeocoris pallens, Franklinothrips vespiformis, Neoseiulus cucumeris, Orius albidipennis, Orius strigicollis,*

Medetera ambigua (, LEWIS 1973, GILLESPIE 1989, BR⊘DSGAARD and HANSEN 1992, MADADI et al. 2007, WU et al. 2014). In Denmark, the control efficiency of *A. cucumeris* and *A. barkeri* was compared under the greenhouse, where *A. cucumeris* was more effective than *A. barkeri* (BR⊘DSGAARD and HANSEN 1992). According to WU et al. (2014), in greenhouse condition, 250 Stratiolaelaos scimitus and Neoseiulus barkeri per m^2 each were effective against onion thrips. The control of *N. cucumeris* against onion thrips was more efficient on sweet pepper than on cucumber and eggplant. This difference may be related to the plant surface structure, and the presence of glandular trichomes, leaf hair, thorns, odours, and spines that may affect the search pattern and the behavioural response of predators (MADADI et al. 2007.

Parasitoids

The most important parasitoids of thrips are endoparasitoids infecting the body of their host and ultimately killing the hosts. The parasitoid species *Ceranisus menes* was significantly more efficient to suppress onion thrips than predators. The control efficiency of parasitoids against onion thrips depends on the host plant species; e.g. in India, control performance of parasitoids on onion was significantly higher than on garlic (JAYANTHI and NIGHOT 2013).

4. MATERIALS AND METHODS

4.1. ESTABLISHING COLONIES OF THE LINEAGES

To ensure a regular supply of individuals for the experiments, pure stock colonies of the *T. tabaci* lineages were maintained on different plant sources in the Department of Entomology, Szent István University in Budapest, Hungary. The arrhenotokous leek -(L1), thelytokous leek -(L2) and arrhenotokous tobacco-associated (T) lineages were maintained on leek (*Allium porrum* L.), cabbage (*Brassica oleracea* L. convar. *capitata* var. *alba*) and tobacco (*Nicotiana tabacum* L.) leaves, respectively (LI et al. 2014, MURAI and LOOMANS 2001). The colonies were maintained at 23°C under long daylight (16L: 8D).

Host plants: Cabbage and tobacco plants were used in this research. Cabbage plants were grown at the Experimental and Research Farm of the Horticultural Science Faculty of Szent István University, and tobacco plants were grown in the plant growing room of the Department of Entomology at Szent István University. Cabbage leaf discs dissected from head forming leaves were used in the bioassays of the two leek-associated (L1 and L2) *T. tabaci* lineages; because these two lineages perform well on this common host plant (LI et al. 2014) and tobacco leaf discs dissected from middle-aged leaves were used in the bioassays of the tobacco-associated (T) *T. tabaci* lineage. The plant parts were carefully examined before introduced to the culture in order to prevent unwanted thrips contamination (thrips-free plant material).

Figure 2: Onion thrips colonies maintained in ventilated containers, (A) arrhenotokous tobacco-(T) on tobacco leaf, (B) thelytokous leek-(L2) on cabbage leaf and (C) arrhenotokous leek-associated (L1) on leek leaf (FARKAS and SOJNOCZKI 2016).

4.2. EFFECTS OF TEMPERATURE AND PHOTOPERIOD ON THE REPRODUCTIVE DIAPAUSE AND LIFETABLE PARAMETRES

Conducting bioassays: To initiate the experiments, random sampled female individuals (10 individuals) were isolated from the stock colonies of each lineages, and reared individually in 2 ml microcentrifuge tubes on cabbage (L1 and L2) and tobacco (T) leaf discs of their preferable host plant and held at 23°C under long daylight (16L: 8D) conditions. Cabbage leaf discs were provided for L1 and L2 lineages as a food source because these two lineages perform well on cabbage plants. To ensure the production of enough eggs for the treatments, these adult females were transferred to new tubes daily until their death. Then the females were preserved in 96% ethanol individually until the lineage was confirmed based on sequences of a mitochondrial COI (mtCOI) product (FARKAS et al. 2020). All these mothers were confirmed as the used lineages for this treatment.

Treatments: Three treatments were set up in environmental growth chambers: (1) 23 °C under long daylight (16L: 8D), (2) 23 °C under short daylight (8L: 16D), and (3) 15 °C under short daylight (8L: 16D). Leaf discs confined into 2 ml microcentrifuge tubes individually and containing eggs of maximum 24 h of age and were exposed to the above treatments because eggs are more sensitive to photophase (NAKAO 1998). Thus, exposure of adults to short daylight is not enough to induce reproductive diapause. The newly hatched first instar larvae were isolated individually in a microcentrifuge tube containing a leaf disc dissected from the lineages' host plant and reared until they became adults. The newly emerged virgin male and female adults were collected daily and kept under the same conditions until they died.

4.2.1. Effect of temperature and photoperiod on preoviposition period and reproductive diapause

Newly emerged virgin female adults of the L1, L2 and T lineages were kept isolated individually and were transferred to a new microcentrifuge tube containing a leaf discs of their preferred host plant every 24 h intervals. The preoviposition period was calculated as the time from adult emergence to the beginning of oviposition. Leaf discs were changed daily until the observation of the first egg using the bottom light of a stereomicroscope (Alpha, NSZ-606, Novel optics, Ningo Yongxin, China). When females began laying eggs, leaf discs were changed regularly at 48 h intervals and diapausing females were provided new leaf discs in a similar way until their death.

To measure the incidence of reproductive diapause, the oviposition of females was monitored in their entire lifetime. The criteria employed to categorize females in reproductive diapause was the failure to oviposit during their lifetime. Females that did not lay a single egg during their lifetime were considered being in a reproductive diapause and females that laid eggs during their lifetime were considered reproducing females. However, some females died within a relatively short period of time without laying a single egg. Those females that died before reaching the age of the upper bound of the 95 % confidence interval of average preoviposition time were excluded from this test. Therefore, the females that lived longer than the upper bound of the 95 % confidence interval of average preoviposition time and produced some eggs were considered reproducing and those that did not lay a single egg as being in reproductive diapause.

4.2.2. Effects of temperature and photoperiod on oviposition period, longevity and fecundity

The length of the oviposition period (i.e., the period between the first and the last egg laid, measured in days), longevity (i.e., the period between the emergence and the death of the adult, measured in days), and fecundity (i.e., total number of eggs laid) were calculated for each female. Females that escaped or those that were accidentally hurt during handling were excluded.

Statistical Analyses: All data analyses were performed using IBM SPSS 25 (SPSS Inc, Chicago, IL, USA). Means of female longevity, fecundity, pre-oviposition and oviposition period were analysed separately using GLM of univariate analysis of variance to test the hypothesis that there would be mean differences between the lineages and treatments. All means are reported with their 95% confidence interval. Prior to analysis, data was checked for normality using nonparametric Kolmogorov-Smirnov and Shapiro-Wilk tests ($P>0.05$) as well as studying skewness and kurtosis. The normality of female longevity and preoviposition data was violated and to normalize the distributions these variables were log transformed. Prior to conducting a series of follow-up t tests, the homogeneity of variance assumption was tested. Independent samples *t*-test was used to compare the significant difference of the variables.

4.3. INBREEDING DEPRESSION AND ITS EFFECTS ON THE LIFETABLE PARAMETERS AND SEX RATIO

To initiate the experiment, 24 female adults were isolated from the stock colonies of L1 and T lineages, and reared individually in 2 ml microcentrifuge tubes on cabbage and tobacco leaf discs, respectively, as a food source and oviposition substrate and held at 23 °C under long daylight (16L: 8D) conditions. L2 lineage was excluded from this experiment, because we were primarily

interested in comparing the effects of brother and sister inbreeding on the lifetable parameters of male producing *T. tabaci* lineages. To ensure the production of enough eggs for the treatments, these adult females were transferred to new tubes daily until their death. Then, females were preserved in 96% ethanol individually until the lineage was confirmed based on sequences of a mitochondrial COI (mtCOI) product (FARKAS et al. 2020). The newly hatched progeny from these mothers were raised individually to adulthood. These progenies used as a parental generation (F_1) for the subsequent inbred line, and assumed that inbreeding coefficient was equal to zero, which was used as a control to compare F_2 and F_3 generations. Thus, F_2 and F_3 generation assumed that inbreeding coefficient was greater than one. The inbreeding coefficient for female haplodiploids that are the product of full sib mating is equal to that of diploids (WRIGHT 1969). Thus, full sibling mating created an inbreeding coefficient (*F*) for inbred haplodiploid females of 0.25 and 0.375 for generation F_2 and F_3, respectively. To measure the intensity of inbreeding depression in the L1 and T lineages, we performed crosses with brother and sister, and mother and son relatedness.

Treatments: Brother and sister inbreeding line was performed for three subsequent generations. Females were randomly chosen from the progeny of the previous generation. Thus, first-generation (F_1) females were daughters of females taken from stock culture and used as a parental generation in the experiment, second-generation (F_2) females were daughters of F_1 females and third-generation (F_3) females were daughters of F_2 females, and therefore females of all generations were assumed to be related.

In order to ensure mating between brother and sister of the L1 and T lineages: a newly emerged F_1 brother and sister produced from the same mother were confined into the same microcentrifuge tube for 48 h. Then the male was removed and its sister was kept isolated individually for the rest of its lifetime. Leaf discs were changed every 48 h and eggs in the leaf discs were counted using the bottom light of a stereomicroscope. Fecundity, egg hatchability (in %), longevity (in days), sex ratio of the progeny was measured. The procedures of brother and sister inbreeding in L1 and T lineage is given in figures 2 and 3, respectively.

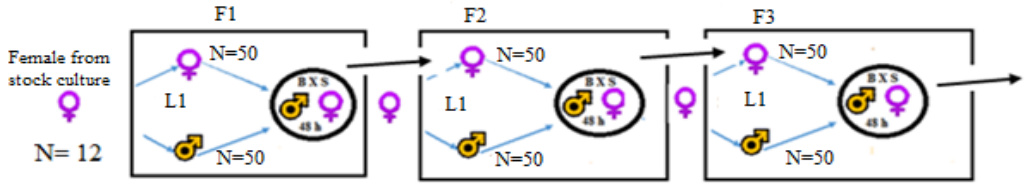

Figure 3: Brother and sister inbreeding scheme in L1 Lineage: 12 females were taken from the stock culture and reared them to produce F_1 progeny. B= brother, S= sister. F_1 brother and sister produced from the same mother were confined into the same microcentrifuge tube for 48 h. The male was removed from the tube after 48h and its mated sister kept reared on tobacco leaf discs and named as F_1 generation. Since then, F_1

females allowed for producing brother and sister to continue the F_2 brother and sister inbreeding and similar procedure was used with F_1 inbreeding line.

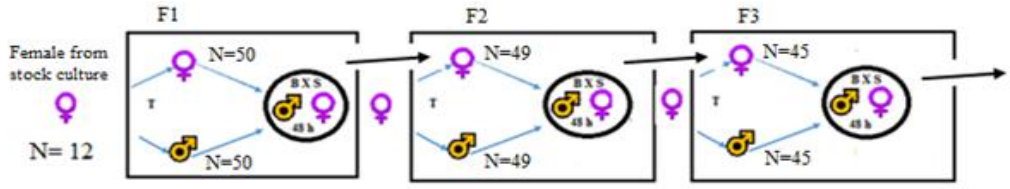

Figure 4: Brother and sister inbreeding scheme of the T lineage: 12 females were taken from the stock culture and reared them to produce F_1 progeny. B= brother, S= sister. F_1 brother and sister produced from the same mother were confined into the same microcentrifuge tube for 48 h. The male was removed from the tube after 48h and its mated sister kept reared on tobacco leaf discs and named as F_1 generation. Since then, F_1 females were allowed to produce brother and sister to continue the F_2 brother and sister inbreeding and similar procedure used with F_1 inbreeding line.

Statistical Analyses: All data analyses were performed using IBM SPSS 25 (SPSS Inc, Chicago, IL, USA). Means of female longevity, fecundity, and egg hatchability rate were analysed separately using GLM of univariate analysis of variance to test the hypothesis that there would be mean differences in inbreeding depression effects on a different generation. All means are reported with their standard deviation. Prior to analysis, data were checked for normality using nonparametric Kolmogorov-Smirnov and Shapiro-Wilk tests ($P>0.05$) as well as studying skewness and kurtosis. The normality of egg hatchability data was violated and to normalize the distributions this variable was arcsign transformed. Prior to conducting a series of follow-up t tests, the homogeneity of variance assumption was tested and Levene's test was accepted. The independent samples *t*-test was used to compare the significant difference of the variables.

4.4. EFFECT OF TEMPERATURE ON SEX RATIO AND LIFETABLE PARAMETERS

Rearing: The arrhenotokous L1 and T lineages were used for this experiment. To produce the known age females from known lineages the following procedures were used: 12 unknown age females were randomly isolated from the stock culture of arrhenotokous L1 and T lineages and reared individually in 2-ml microcentrifuge tubes on cabbage head and tobacco leaf discs, respectively. Eggs in the leaf discs were counted by using the bottom light of a stereomicroscope. The progeny was raised to adulthood in isolation since the newly emerged larvae. In order to ensure mating in the L1 and T lineages a newly emerged female and male adult was confined into the same microcentrifuge tube for 24 h. Then the male was removed and the female adult was kept isolated individually for the rest of its life.

Treatments: In the laboratory, three temperature ranges such as 15, 23, and 30 °C were established to test the effects of temperature on the sex ratio and lifetable parameters of the

arrhenotokous leek- (L1) and tobacco-associated (T) *T. tabaci* lineages and the test was performed under controlled environmental growth chamber with long daylight (16L: 8D).

4.4.1. Effect of temperature on the pre-oviposition, fecundity, egg hatchability and longevity

The newly emerged female adults of the L1 and T lineages were exposed to 15, 23, and 30°C. Female adults were transferred to a new microcentrifuge tube containing a leaf discs of their preferred host plant in every 24 h intervals for their entire lifetime. The eggs in the leaf tissue were counted using the bottom light of a stereomicroscope. The pre-oviposition period of the L1 and T mothers (n=17, 19) at 15°C, (n=38, 35) at 23°C, and (n=37, 45) at 30°C, respectively, was calculated as the time between adult emergence to the observation of the first egg, measured in days. When females began laying eggs, leaf discs were changed regularly at 24 h intervals. Fecundity (i.e., the total number of eggs laid) of the L1 and T mothers (n=17, 39) at 15°C, (n=38, 35) at 23°C and (n=37, 45) at 30°C, respectively, was calculated for each female. Egg hatchability of the L1 and T mothers (n=17, 19) at 15°C, (n=38, 35) at 23°C and (n=37, 45) at 30°C, respectively, was calculated as the ratio of the hatched eggs and total number of eggs per female, expressed in percent. Longevity (i.e., the period between the emergence and the death of the adult) of the L1 and T mothers (n=46, 45) at 15°C, (n=39, 35) at 23°C and (n=38, 45) at 30°C, respectively, was measured in days.

4.4.2. Effect of temperature on the sex ratio

The development of the progeny produced by mated females was terminated in either the first or second instar stage and all of the larvae were preserved in 75% ethanol. At a later period, the preserved larvae were slide mounted in drops of Berlese mounting medium. To dry the specimens, the slides were kept in an oven at 50°C for 2 days. The nymphal progenies were collected from the mothers of the L1 and T lineages (n=17, 15) at 15°C, (n=39, 34) at 23°C, (n=38, 45) at 30°C, respectively. The number of larvae identified as male and female from each temperature treatments are presented in Table 21.

Statistical analysis: All data analyses were performed using IBM SPSS 25 (SPSS Inc, Chicago, IL, USA). To detect the mean differences between the effects of treatments, sex ratio and longevity were analysed separately by one-way ANOVA. Pre-oviposition period, fecundity and egg hatchability were tested by one-way multivariate ANOVA (MANOVA) that was followed by univariate ANOVA tests with Bonferroni's correction. All means are given with their standard deviations in Tables 2-6. Prior to analysis, data were checked for normality. The residuals for

longevity of L1, fecundity and egg hatchability of T lineages were normally distributed, and there were no data transformation for these variables. While, the normality of the residuals for sex ratio, pre-oviposition of L1 and T, fecundity and egg hatchability of L1 and longevity of T was violated. To normalize the distributions of the data, sex ratio was transformed by ln for L1 and T, longevity was transformed by ln for T, pre-oviposition of L1 and T were transformed by reciprocal transformation, while fecundity of L1 were transformed by square-root and the egg hatchability of L1 was squared. The normality of the residuals was then confirmed in all cases by their skewness and kurtosis because all of their absolute values were below 1. The homogeneity of variance assumption was tested for all response variables by Levene's test that revealed homoscedasticity acceptance for sex ratio, longevity, and for multiple pairwise comparisons, Tukey's post hoc test was performed, while the homogeneity of Levene's test revealed homoscedasticity violations for pre-oviposition, fecundity, and egg hatchability, therefore, for multiple pairwise comparisons, Games-Howell's post hoc test was performed. To detect the log-linear relationship of temperature with sex ratio and with longevity, Pearson's correlation coefficients were calculated and tested against significance by Student's t test.

4.5. THE EXISTENCE OF DEUTEROTOKOUS REPRODUCTION MODE IN THE *T. TABACI* LINEAGES

4.5.1. Pupal insemination

To initiate the experiment, twelve adult females were isolated from the stock culture of L1 and T lineages. The isolated females were reared individually in 2 ml microcentrifuge tubes with a single leaf discs (cabbage leaf discs for L1 and tobacco leaf discs for T) lineages and the leaf discs were replaced every 24 hours. The rearing has been carried out under the environmental growth chamber at 23 °C under (16L:8D). The eggs in the leaf discs were checked with bottom light of stereomicroscope and the reproducing females were transferred to new tubes daily. Then the dead females were preserved in 96% ethanol individually until the lineage was confirmed based on sequences of a mitochondrial COI (mtCOI) product (FARKAS et al. 2020). The hatched first and second instar larvae were individually transferred to new tubes with fresh leaf discs and raised to the pupal stage.

Experimental design: 42♀ pupae from L1 and 44♀ pupae from T lineages were used. A single female pupa and male adult were confined into the same microcentrifuge tube for 24 hours. The response of female pupa to the male adult upon mating was checked using a stereomicroscope. A male from the tube that contained the female pupa has been removed, and the female pupa kept isolated individually in the tube until it became adult. Then, the newly emerged adult females were

reared for 8 to 10 days to produce eggs and all the newly hatched first and second instar larvae were collected and preserved in 75 to 80 percent ethanol alcohol. Since then, the preserved first and second instar larvae of L1 and T lineages were slide mounted to confirm their sex.

Larvae identification key

The accepted larvae identification key for Thripidae was described by (SPEYER and PARR, 1941). The major differences between first and second instar larvae are based on the number of setae on their II to VII abdominal segments, number of setae on their pronotum and the presence or absence of spiracles on the abdominal segment II (**Figure** 5 A, B and **Figure** 6 C, D).

First instar larvae are small in size as compared to the second instar larvae, comprise of two pairs of sternal setae on their abdominal segments II to VII and six pairs of setae on the pronotum (VIERBERGEN et al. 2010) and also contain a spiracle on the abdominal segment II (KIRK 1987).

Second instar larva is larger and fat body size as compared to first instar larvae. This stage consists of 3 pairs of sternal setae on the abdominal segments II-VII, two pairs of spiracles and seven pairs of setae on the pronotum (VIERBERGEN et al. 2010). It has no spiracle on the abdominal segment II (KIRK 1987).

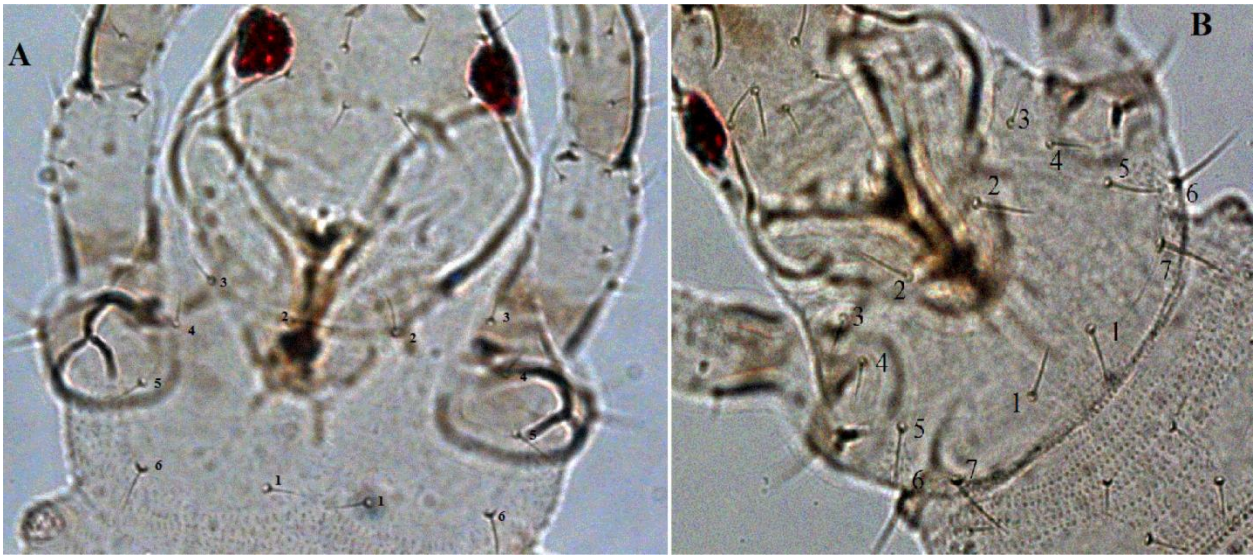

Figure 5; (A) Indicated that the first instar larvae and the numbers are used to indicate the pairs of setae on the pronotum; (B) Indicated that the second instar larvae and the numbers are used to indicate the pair of setae on the pronotum (WOLDEMELAK 2019).

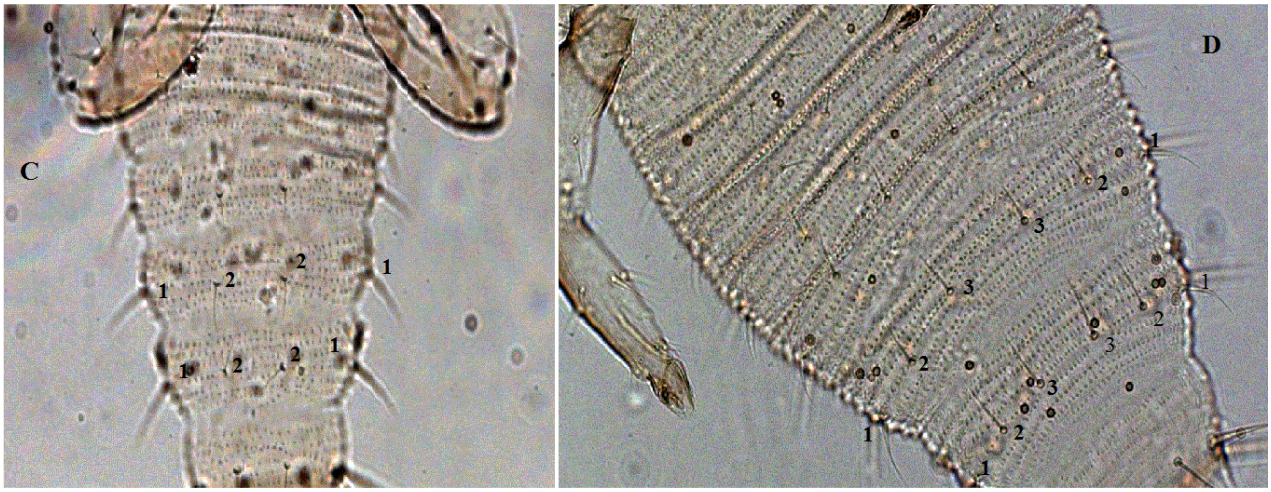

Figure 6; (C) Indicated that the first instar larvae and the numbers are used to indicate the pairs of setae on the ventral part of the abdomen; (D) Indicated that the second instar larvae and the numbers are used to indicate the pair of setae on the ventral part of the abdomen (WOLDEMELAK 2019).

Sex identification key

The sex of immature stages in the *T. tabaci* is determined based on their number of setae on the abdominal segment IX. The first instar larvae male exhibit 4 pairs and females exhibit 3 pairs of setae on their IX abdominal segment (**Figure** 7), whereas second instar larvae male exhibit five pairs, and female exhibit four pairs of setae on their IX abdominal segment (**Figure** 8). (VIERBERGEN et al. 2010).

All the feature and sex identification of first and second instar larvae were determined using an optical compound microscope with 400x, 600x and 1000x magnifications. The determination of pupal insemination was based on the sex of its progeny upon adult. Therefore, female pupa was considered as not inseminated by adult male if all the progenies are males (males are produced from unfertilized eggs).

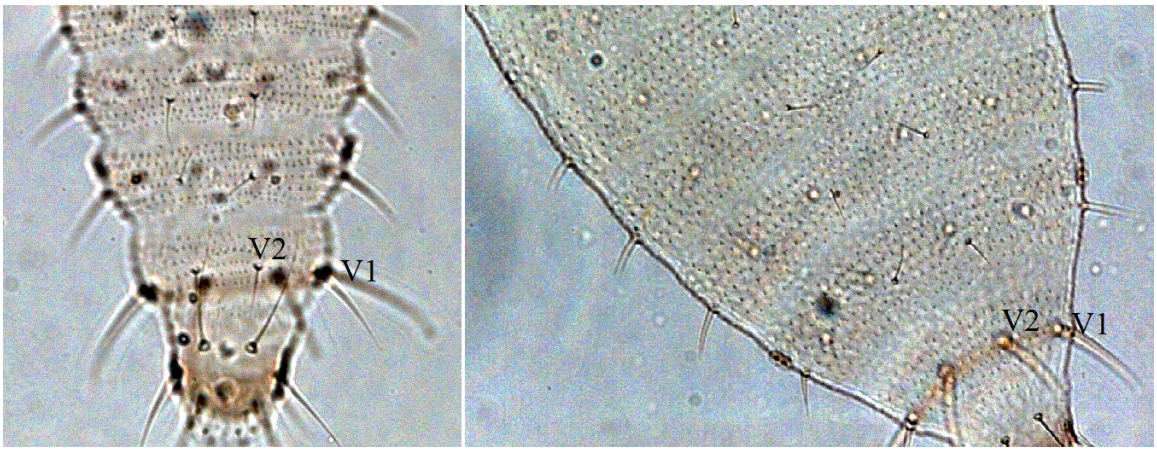

Figure 7 (E): First instar male. The numbers are used to indicate the pairs of setae on both dorsal and ventral abdominal segment IX (WOLDEMELAK 2019)

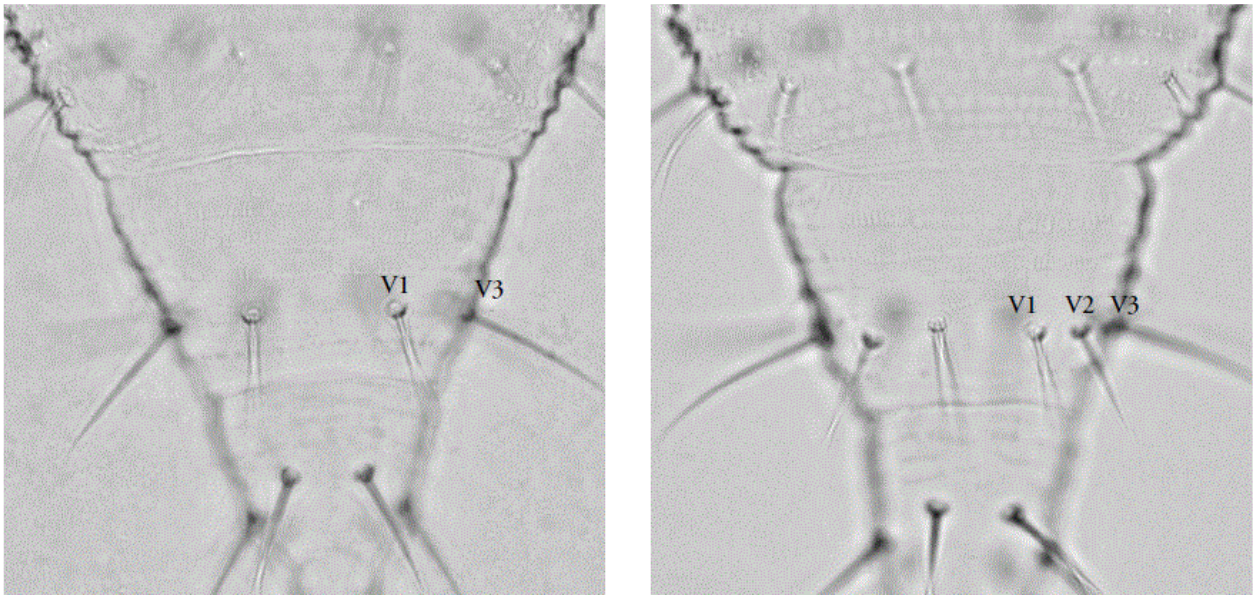

Figure 8 (F): Second instar male. The numbers are used to indicate the pairs of setae on both dorsal and ventral abdominal segment IX (WOLDEMELAK 2019)

4.5.2. Mother-son inbreeding

To test whether a mother and son inbreeding is the factor to induce a deuterotokous reproductive mode of the L1 and T lineages: 10 female adults were isolated randomly from each stock colonies of the L1 and T lineages, and reared individually in 2 ml micro-centrifuge tubes. Cabbage and tobacco leaf discs were provided for L1 and T lineages, respectively, to serve as a food source and oviposition site. Although, before the cabbage and tobacco leaf discs provided as a food and oviposition site: the dissected cabbage head and tobacco leaves were checked using the bottom light of a stereomicroscope to ensure that the leaf discs were not contaminated by other thrips species before experimentation. To ensure the production of ample eggs for the treatments, these adult females were transferred to new tubes daily until their death. Then the females were preserved in 96% ethanol individually until the lineage was confirmed based on sequences of a mitochondrial COI (mt COI) product (FARKAS et al. 2020). The newly hatched progeny from these mothers were raised to adulthood. These progenies were considered as F_1 generation and used as a parental generation for the subsequent inbred line. Thus, all the tested inbred generations were assumed to be related.

To ensure a son for virgin female: 30 virgin single adult females were isolated from the F_1 females and reared individually on their preferable food leaf discs for 2 days at 23 °C. As they were virgins, their eggs were unfertilized and assume to be developed into sons. Then the reproducing females were placed at 15 °C. At this low temperature, their longevity is increased which increases their chance for mating with their own son. When the son became adults, single mother and son were confined into the same microcentrifuge tube for 48 h. Then the male was

removed and the female adult was kept isolated individually in the rest of its lifetime. The progeny produced from these mothers were considered as F_1 mother and son inbred line and their subsequent daughters were collected for F_2 mother and son inbreeding. Mother and son inbreeding has tested for two subsequent generations such as (F_1) females were daughters of females taken from stock culture and used as a parental generation in the experiment and (F_2) females were daughters of F_1 females.

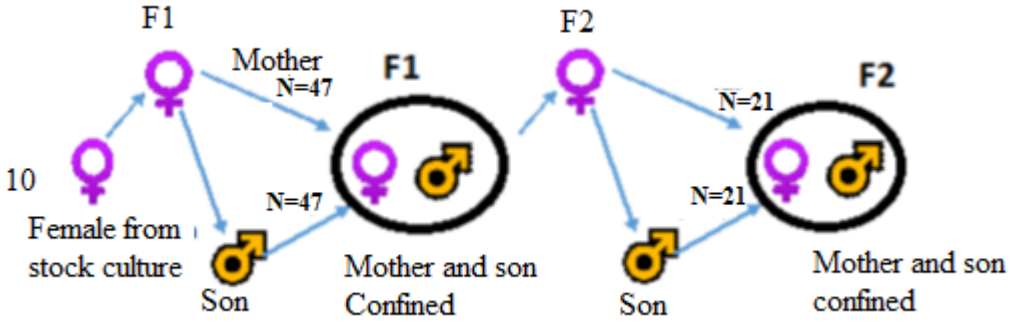

Figure 9: Mother and son inbreeding scheme in L1 lineage: 10 females were taken from the stock culture and reared them to produce F_1 progeny. Then, 47 F_1 virgin females were reared to produce sons and when the son became an adult; both mother and son were confined in the same tube for 48 h. The male was removed from the tube after 48h and its mother kept reared on tobacco leaf discs and named as F_1 generation. Since then, F_1 females were allowed to produce a son to continue the F_2 mother and son inbreeding and similar procedure used with F_1 inbreeding line.

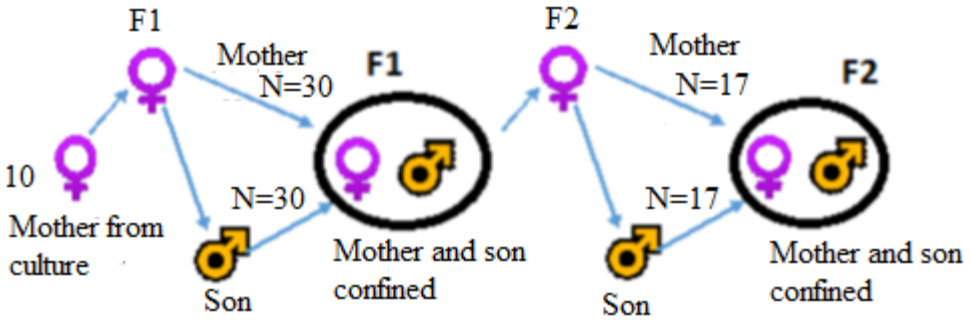

Figure 10: Mother and son inbreeding scheme in T lineage: 10 females were taken from the stock culture and reared them to produce F_1 progeny. Then, 30 F_1 virgin females were reared to produce sons and when the son became an adult; both mother and son were confined in the same tube for 48 h. Male was removed from the tube after 48h and its mother kept reared on tobacco leaf discs and named as F_1 generation. Since then, F_1 females allowed producing a son to continue the F_2 mother and son inbreeding and similar procedures were used with F_1 inbreeding line.

4.6. FIGHTING BEHAVIOUR OF MALE IN *T. TABACI*

Rearing: To initiate the experiment, twenty female adults of unknown age were isolated from the stock colonies of each lineage and reared individually in 2 ml microcentrifuge tubes on leaf discs of their preferable host plant. L1 females were given cabbage and T female's tobacco.

To ensure the production of ample male progeny for the experiment, these adult females were transferred to new tubes daily until their death. Then the females were preserved in 96% ethanol individually until the lineage was confirmed based on sequences of a mitochondrial COI (mt COI) product (FARKAS et al. 2020). The newly hatched first instar larvae were individually transferred to new microcentrifuge tubes and kept at 23 °C under a long photoperiod (16L: 8D). Upon reaching maturity, adult males were collected daily for the purposes of the experiment. These males were isolated and kept individually in a separate micro-centrifuge tube. This way ensured that no males had any contact with other males.

Bioassay: Arena technique as described by KIRK (1987) was adapted for this experiment. Transparent PCR tube caps were used to form the arena. A total of 80 males (40 belonged to L1 and 40 belonged to T lineages) were used for this experiment, and the pairs of males were 2, 5, 8, 10, 12 days old in four replications. Two males with no previous fighting experience were transferred into the PCR tube cap, and a microscopic glass coverslip was immediately sealed onto the PCR tube caps to form the roof of the arena and this way was used to prevent males from escaping.

Video recording: A Euromex VC.3036 video camera was placed above the arena on a stereomicroscope at a height of 15 cm that enabled it to view the whole arena. This was connected to a video recorder hp computer and each experiment was recorded with a resolution of 1920X1080 for a duration of 10 min. Data was obtained from the recorded video. Each recording had a different arena.

Observations: A total of 40 video recordings (20-20 for L1 and T, with 40 individuals for each lineages) were observed. Fighting was defined as observations of contact between two males with antennal bouts, abdominal flicking, grabbing and flipping, where these actions took more than 1 second. The percentage of fighting males, fighting frequency (number of fights recorded in the arena during the observation period), pre-fight period (the time before the first fight), duration of fight and re-fighting time interval (the time between two consecutive fights) were recorded during each 10-minute observation.

Statistical Analyses: - All statistical analyses were performed using SPSS software (IBM Inc, Chicago, IL, USA). Ages were used as a block factor to eliminate its source of variability on the general fighting performance of the lineages (GOMEZ and GOMEZ 1984). Means of fighting frequency, pre-fight period, duration of fight and of refighting time interval were analysed separately using GLM of multivariate analysis of variance to test the mean differences between the lineages. All means have been given with their standard deviations. All the parameters were transformed by natural logarithm (ln (x)) functions. The normality of the residuals was confirmed

by using nonparametric Kolmogorov-Smirnov and Shapiro-Wilk tests (P> 0.05). The Games-Howell post hoc test was used to compare the significant difference of the variables.

5. RESULTS AND DISCUSSION

5.1. EFFECTS OF TEMPERATURE AND PHOTOPERIOD ON REPRODUCTIVE DIAPAUSE AND LIFETABLE PARAMETERS

5.1.1. Effects of temperature and photoperiod on the preoviposition period

The preoviposition periods of females of the L1, L2 and T lineages were significantly influenced by temperature and photoperiod treatment ($F(2, 239) = 239.621$; $P < 0.001$, $F(2, 117) = 177.917$, $P < 0.001$, $F(2, 111) = 52.398$, $P = 0.001$, respectively). The preoviposition periods of L2 lineage were significantly different between 8L: 16D and 16L: 8D at 23 °C, but there were no significant difference in the L1 and T lineages (**Table** 5).

Additionally, the preoviposition periods of all three lineages were significantly longer with decreasing temperature and lengthening dark period settings. The average preoviposition periods of all three lineages ranged from 9.03 to 27.72 days under 8L: 16D at 15 °C. Ten times longer preoviposition periods were observed in the L1 lineage under 8L: 16D at 15 °C than those females reared under 8L: 16D at 23°C (**Table** 6).

Table 5: Effect of photoperiod on the preoviposition period of *T. tabaci* lineages (days) (mean ± 95 % confidence interval).

Treatment	L1 lineage	L2 lineage	T lineage
23°C, l6L:8D	2.55±0.2a (n=49)	2.4±0.3a (n=48)	2.76±0.3a (n=49)
23 °C, 8L:16D	2.78±0.4a (n=50)	4.5±0.5b (n=50)	3.37±1.1a (n=29)

Note: Different letters indicate a significant difference between treatments (independent samples t-test, $p < 0.05$).

Table 6: Effect of temperature on the preoviposition period of *T. tabaci* lineages (days) (mean ± 95 % confidence interval).

Treatment	L1 lineage	L2 lineage	T lineage
23 °C, 8L:16D	2.78±0.4a (n=50)	4.5±0.5a (n=50)	3.37±1.1a (n=29)
15 °C, 8L:16D	27.72±6.9b (n=11)	17.8±2.8b (n=22)	9.03±1.6b (n=32)

Note: Different letters indicate a significant difference between treatments (independent samples t-test, $p < 0.05$).

In this work, the preoviposition periods of females in the L2 lineage were significantly longer when the females were exposed to 8L: 16D at 23 °C, but there was no significant difference in the L1 and T lineages. BR∅DSGAARD (1994) found no difference in preoviposition period of *F. occidentalis* between 4L: 20D, 8L: 16D and 16L: 8D at 25 °C. The variation in photoperiod

response among *T. tabaci* lineages suggests that adaptation in different photo-regime might be another variability between the lineages. Thus, L2 lineage may have experienced a physiological adaptation to long daylight only whereas; L1 and T lineages may have experienced a physiological adaptation to both short and long daylight at optimum temperatures of 23 °C. On the other hand, a significant difference in preoviposition period of females in all lineages was observed between 15 and 23 °C under 8L: 16D. It indicates that short daylight does not act in isolation to influence the length of the preoviposition period of females in the L1 and T lineages. More specifically, we suggest that the preoviposition period's of females in the L1 and T lineages determined by the effect of both low temperature and short daylight. MURAI (2000) found longer preoviposition period of females in the L2 lineage at 15 °C. Longer preoviposition period under 10L: 14D at 20 °C, but no difference between 10L: 14D and 16L: 8D at 15 °C has been reported in *F. occidentalis* (ISHADA et al. 2003). Long daylight (L16:D8) and high temperature (29 °C) increased the preoviposition periods of *Megalurothrips sjostedti* (Trybom) (Thysanoptera: Thripidae) and absence of egg laying at these conditions indicates some evidence of reproductive diapause (EKESI et al. 1999). Longer preoviposition periods (19 days) have also been reported in *Heliothrips haemorrhoidalis* (Bouché) (Thysanoptera: Thripidae) at 15 °C (RIVNAY 1995). In this result, shortest preoviposition periods were 9.03 days for T lineage and longest preoviposition periods were 27.7 days for L1 lineage under 8L: 16D at 15°C. MURAI (1987) has found longer preoviposition period in *F. intonsa* under 13L: l1D (2.8 days) than 14L: 10D (3.5 days) at 20 °C. The suggested factor for delaying the preoviposition period under short daylight and low temperature is most likely due to the maturation of ovaries. Ovaries might need a longer time to mature under short daylight, which leads to delayed egg maturation. Insects exposed to low temperature and short photoperiod enter a state of arrested development, lowered metabolism, and increased stress resistance. These all together altered carbohydrate, protein, and lipid metabolism and slowed senescence of the intestine and finally, such physiological and behavioural adjustments lead to retard ovary development (KUBRAK et al. 2014). The effect of photophase on the maturation of ovaries has been well discussed by (LEWIS 1973). In this study in general; we expect that delaying the preoviposition period due to the effect of short daylight would probably lead to a reduction in the population size of the lineages.

5.1.2. Effects of temperature and photoperiod on reproductive diapause

Reproductive diapause was detected for 40 % of the tested females in the T lineage under 8L: 16D at 23 °C, however, reproductive diapause was not detected in the L1 and L2 lineages under 8L: 16D at 23 °C. However, reproductive diapause in all three lineages was detected under

8L: 16D at 15 °C). There was no significant difference in the incidence of reproductive diapause females in the T lineage between 23 and 15 °C under 8L: 16D (**Table** 7).

Table 7: Effect of temperature on the incidence of reproductive diapause of *T. tabac*i lineages (%).

Treatment	L1 lineage	L2 lineage	T lineage
23 °C, 8L:16D	-	-	40a (n=21/50)
15 °C, 8L:16D	50 (n=11/22)	42 (n=16/38)	28a (n=14/48)

Note: Similar letters indicate no significant difference between treatments (independent samples t-test, $p > 0.05$).

Photoperiod has been recognized for a number of years as one of the chief environmental factors regulating diapause in insects (MCMULLEN 1967). Because photoperiods can provide the most reliable signals of seasonal change and both photoperiod and temperature are considered as the most influential environmental factors for diapause induction (MOUSSEAU and DINGLE 1991, MOUSSEAU and FOX 1998). In this experiment, 8L: 16D at 23 °C induced reproductive diapause in the T lineage but neither the L1 nor the L2 lineages entered reproductive diapause. This result has been supported by (NAKAO 1994) where 10L: 14D at 25°C induced reproductive diapause in *Thrips nigropilosus* (Uzel) (Thysanoptera: Thripidae). In addition, in present study reproductive diapause was detected in all three lineages when the temperature was dropped to 15 °C under 8L: 16D. NAKAO (1998) found reproductive diapause in *Thrips setosus* (Moulton) (Thysanoptera: Thripidae) under 10L: 14D at 18 °C. Therefore, reproductive diapause seems to occur in the T lineage likely due to the effect of short daylight, and in the L1 and in the L2 lineages likely due to low temperature. Interactions between low temperature and short photoperiod are known to induce reproductive diapause (MURAI 1987). MURAI (1987) has also reported that *F. intonsa* females under 10L: 14D at 23 °C produce eggs, but 100 % of these females entered reproductive diapause when the temperature was dropped to 20, 16 and 12 °C under 10 h daylight. HODEK and CERKASOV (1961) reported that interactions of short photoperiods and low temperatures induced diapause in *Coccinella novemnotata (*Herbst) (Coleoptera: Coccinellidae). KAMM (1972) reported reproduction diapause induced in the *Anaphothrips obscurus* (Müller) (Thysanoptera: Thripidae) by exposing larvae to short days (10L: 14D) and LEWIS (1973) observed it in *Limothrips cerealium (Haliday)* (Thysanoptera: Thripidae). The incidence of reproductive diapause varied across different geographical locations in the *Haplothrips brevitubus* (Karny) (Thysanoptera: Phlaeothripinae) (FUJIMOTO 2014). More than 90 % of *H. brevitubus* females collected from the Iwate and Kyoto region entered reproductive diapause under a photoperiod of less than 14 h daylight, whereas less than 50 % of females collected from

Kagoshima region entered reproductive diapause under similar photoperiods (FUJIMOTO et al. 2014).

5.1.3. Effects of temperature and photoperiod on oviposition period

The oviposition periods of females of the L1, L2 and T lineages were significantly influenced by temperature and photoperiod treatment ($F_{(2,107)} = 26.142$, $P < 0.001$, $F_{(2,117)} = 21.192$, $P < 0.001$, $F_{(2,111)} = 12.133$, $P < 0.001$, respectively). Length of oviposition periods of the L1 and T lineages were significantly different under 8L: 16D at 23 °C, but there was no significant difference in the L2 lineage (**Table** 8). In all three lieages, there was no significant difference between 15 and 23 °C under 8L: 16D (**Table** 9).

Table 8: Effect of photoperiods on oviposition period of *T. tabaci* lineages (days) (mean ± 95 % confidence interval).

Treatment	L1 lineage	L2 lineage	T lineage
23°C, l6L:8D	23.6±1.9b (n=49)	20.31±1.5b (n=48)	20.5±1.5b (n=49)
23 °C, 8L:16D	14.02±1.8a (n=50)	16.8±1.9ab (n=50)	14.9±3.2a (n=29)

Note: Different letters indicate a significant difference between treatments (independent samples t-test, $p < 0.05$).

Table 9: Effect of temperature on oviposition period of *T. tabaci* lineages (days) (mean ± 95 % confidence interval).

Treatment	L1 lineage	L2 lineage	T lineage
23 °C, 8L:16D	14.02±1.8a (n=50)	16.8±1.9ab (n=50)	14.9±3.2a (n=29)
15 °C, 8L:16D	10.72±2.7a (n=11)	13.75±5.4a (n=22)	14.71±3.1a (n=32)

Note: Different letters indicate a significant difference between treatments (independent samples t-test, $p < 0.05$).

Our result indicates that the oviposition periods of all lineages were significantly decreased under 8L: 16D at 23 °C). Females of *H. brevitubus* exposed to 16L: 8D at 20 °C initiated oviposition within 15 days after adult emergence, while those exposed to short-day conditions entered reproductive diapause (FUJIMOTO et al. 2014). In addition to decreasing oviposition period, all three lineages were still able to produce fewer eggs under short daylight. The decline of oviposition period may be related to low uptake of improved diet induced by short daylight. The quality of food they feed and oviposition period might be interlinked with photoperiod. Longer oviposition periods in the thrips species are usually dependent on the quality of food (HULSHOF et al. 2003). WHITTAKER and KIRK (2004) found that the amount of pollen consumption and

oviposition period all increased with increasing photophase and decreased with decreasing photophase. Food quality has also been shown to influence egg production in *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) (MCMULLEN 1967). Irregular and sporadic egg production under long daylight (16L:8D) at 29 °C was reported in *M. sjostedti* (EKESI et al. 1999). In this result, the egg production in all lineages under a short daylight (8L: 16D) at 15 °C was also irregular and sporadic and to lay the next egg females had 5 to 8-day oviposition intervals. Females under these conditions laid very few eggs. Low temperature and lengthy dark periods might have affected the morphogenesis of embryo and egg maturations: which caused irregularity and sporadic egg production.

5.1.4. Effects of temperature and photoperiod on the longevity

The longevity of females in the L1 and T lineages were significantly influenced by temperature and photoperiod treatment ($F(2,107) = 19.606$, $P < 0.001$ and $F(2,111) = 29.745$, $P < 0.001$, respectively), while it was no significantly different in the L2 lineage ($F(2,117) = 2.768$, $P > 0.05$). The average longevity of reproducing females in the T lineage increased significantly under 8L: 16D at 23 °C than those females under 16L: 8D. Nevertheless, there was no significant difference in the L1 and L2 lineages between 8L: 16D and 16L: 8D at 23 °C. T linages had about ten day's longer longevity under short daylight than L2 lineages (**Table** 10).

Furthermore, all three lineages had significantly longer longevity under 8L: 16D at 15 °C than under 8L: 16D at 23 °C. All reproducing females in the L1 and L2 lineages reared under 8L: 16D at 15 °C died within 49 days whereas, reproducing females in the T lineage died within 76 days. Reproducing females in the T lineage had twofold longer longevity under 8L: 16D at 15 °C than those females reared under 8L: 16D at 23 °C (**Table** 11).

Table 10: Effect of photoperiod on longevity of reproducing females of *T. tabaci* lineages (days) (mean ± 95 % confidence interval).

Treatment	L1 lineage	L2 lineage	T lineage
23°C, l6L:8D	29.51±2.2a (n=49)	25.69±1.8a (n=48)	29.76±1.2a (n=49)
23 °C, 8L:16D	30.9±1.3a (n=50)	28.52±2.5a (n=50)	38.06±4.3b (n=29)

Note: Different letters indicate a significant difference between treatments (independent samples t-test, $p < 0.05$).

Table 11: Effect of temperature on longevity of reproducing females of *T. tabaci* lineages (days) (mean ± 95 % confidence interval).

Treatment	L1 lineage	L2 lineage	T lineage
23 °C, 8L:16D	30.9±1.3a (n=50)	28.52±2.5a (n=50)	38.06±4.3a (n=29)
15 °C, 8L:16D	48.9±8.7b (n=11)	34.22±6.3b (n=22)	76.89±12.4b (=32)

Note: Different letters indicate a significant difference between treatments (independent samples t-test, $p < 0.05$).

Longevity of diapausing females in the T lineage was significantly different under 8L: 16D at 15° C, but there was no significant difference under 8L: 16D at 23 °C (**Table** 12). On the other hand, there was no significant difference in longevity between dispausing and reproducing females in the L1 and L2 lineages under 8L: 16D at 15 °C (**Table** 13).

Table 12: Effect of photoperiod on longevity of diapausing and reproducing females (days) (mean ± 95 % confidence interval).

Treatment	L1 lineage		L2 lineage		T lineage	
	Diapausing	Reproducing	Diapausing	Reproducing	Diapausing	Reproducing
23°C, l6L:8D	-	29.51±2.2 (n=49)	-	25.69±1.8 (n=48)	-	29.76±1.2a (n=49)
23 °C, 8L:16D	-	30.9±1.3 (n=50)	-	28.52±2.5 (n=50)	39.67±5.7A(n=21/50)	38.06±10.3Ab (n=29)

Note: Different letters indicate a significant difference between treatments (independent samples t-test, $p < 0.05$). Small letters indicate a comparison between diapausing and reproducing females between the treatment and upper letters indicate comparison between diapausing and reproducing females within the treatment.

Table 13: Effect of temperature on longevity of diapausing and reproducing females (days) (mean ± 95 % confidence interval).

Treatment	L1 lineage		L2 lineage		T lineage	
	Diapausing	Reproducing	Diapausing	Reproducing	Diapausing	Reproducing
23 °C, 8L:16D	-	30.9±1.3 (n=50)	-	28.52±2.5 (n=50)	39.67±5.7Aa(n=21/50)	38.06±10.3Aa (n=29)
15 °C, 8L:16D	50.64±6.8A(n=11/22)	48.9±1.6A (n=11/22)	36±4A(n=16/38)	34.22±4.9A (n=22)	97±17.8Bb (n=14/50)	76.89±3.3Ba (n=32)

Note: Different letters indicate a significant difference between treatments (independent samples t-test, $p < 0.05$). Small letters indicate a comparison between diapausing and reproducing females between the treatment and upper letters indicate comparison between diapausing and reproducing females within the treatment.

Longevity of reproducing females in the T lineage was significantly affected by 8L: 16D at 23 °C. However, the longevity of reproducing females in the L1 and L2 lineages was not affected by 8L: 16D at 23 °C. Adult longevity in all three lineages were increased under short daylight (8L: 16D) at 15 °C than those females reared under short daylight (8L: 16D) at 23 °C. Longest longevity under short daylight (4L:20D) at 25 °C has been reported in *F. occidentalis* (BRODSGAARD 1994) and adult longevity increased with decreasing temperature (14°C) under 12L:12D in *M. sjostedti* (Trybom) (EKESI et al. 1999) and (10 °C*)* under 16L:8D in *Thrips obscuratus* (Crawford) (Thysanoptera: Thripidae) (TEULON and PENMAN 1991). In our result, there was longevity difference between reproducing and diapausing females, where reproducing females showed shorter longevity than diapausing females and it could be due to the direct relationship between fecundity and longevity. Because fecundity is a key factor in terms of reducing longevity. Therefore, diapausing females could have longer longevity due to the trade-off of lower investment in producing eggs and reproducing females could have shorter longevity due to the overall cost of investment in producing eggs. Having longer longevity during an unfavourable season would probably help them to build up their population immediately for the next favoured season. The possible reasons for the variations of longevity among the lineages might be due to the geographic origin resulting from local adaptation to ambient climatic conditions and it might be one of the differences within the *T. tabaci* lineages.

5.1.5. Effects of temperature and photoperiod on fecundity

The mean fecundity rates of reproducing females in the L1, L2 and T lineages were significantly influenced by temperature and photoperiod treatments ($F(2, 107) = 137.785$, $P < 0.001$, $F(2,117) = 82.063$, $P < 0.001$, and $F(2,111) = 120.55$, $P < 0.001$, respectively). In all three lineages, the lowest fecundity rates were recorded under 8L: 16D at 23 °C as compared with the fecundity rates under 16L: 8D at 23 °C. Maximum and minimum fecundity were 89.3 and 39.34 eggs under long daylight (16L: 8D) and short daylight (8L: 16D) at 23 °C, respectively (**Table** 14).

Similarly, in all three lineages the lowest fecundity rates were recorded under 8L: 16D at 15 °C as compared with the fecundity rates under 8L: 16D at 23 °C Maximum and minimum fecundity were 46.94 and 7 eggs under short daylight (8L: 16D) at 23 and 15 °C, respectively (**Table** 15).

Table 14: Effect of photoperiod on fecundity of *T. tabaci* lineages (days) (mean ± 95 % confidence interval.

Treatment	L1 lineage	L2 lineage	T lineage
23°C, l6L:8D	89.30±5.5b (n=49)	80.31±8.3b (n=48)	86.76±6.6b (n=49)
23 °C, 8L:16D	40.14±5.4a (=50)	46.94±4.3a (n=50)	39.34±10.3a (n=29)

Note: Different letters indicate a significant difference between treatments (independent samples t-test, $p < 0.05$).

Table 15: Effect of temperature on fecundity of *T. tabaci* lineages (days) (mean ± 95 % confidence interval.

Treatment	L1 lineage	L2 lineage	T lineage
23 °C, 8L:16D	40.14±5.4b (=50)	46.94±4.3b (n=50)	39.34±10.3b (n=29)
15 °C, 8L:16D	7.00±1.6a (n=11)	13.85±4.9a (n=22)	17.87±3.3a (n=32)

Note: Different letters indicate a significant difference between treatments (independent samples t-test, $p < 0.05$).

In all lineages, fecundity was decreased under 8L: 16D at 23°C. Thus, a short daylight period is likely to have a direct negative effect on the fecundity of all *T. tabaci* lineages. Furthermore, sharp fecundity reduction was recorded due to low temperature (15 °C) under 8L: 16D. MURAI (2000) and SAKIMURA (1937) found that temperature is a factor to increase and decrease the fecundity of thelytokous females. Fecundity decreased in *F. occidentalis* under short daylight (WHITTAKER and KIRK 2004) and *T. nigropilosus* (NAKAO 1994), where fecundity was dropped under short daylight and low temperature. Fewer eggs were laid per female per day under short photoperiod than long photoperiod at 15°C, but no significant difference in the total number of eggs was observed between the two photoperiods (ISHIDA et al. 2003). During our experiment, there were fewer symptoms of damage on the leaf discs under 8L: 16D at 15 °C than under 16L: 8D 23 °C. This has implied that the feeding level of these lineages is directly interlinked with the temperature and length of the photo phase. MURAI (1987) has reported that the general activity, including feeding activity of thrips, is known to be higher in long daylight than in short daylight. Thus, the adult activity and amount of food they feed could be correlated with decreased or increased fecundity in *T. tabaci* lineages. Under short daylight, food intake diminishes drastically, but circulating and stored carbohydrates and lipids are elevated (KUBRAK et al. 2014). WHITTAKER and KIRK (2004) have also mentioned the walking, pollen consumption, and oviposition of the western flower thrips is diurnal. KIRK (1997) has also reported that many phytophagous thrips species mature and lay eggs each day, and can only do this if they obtain

sufficient nutrients. The other factor might be the synthesis of Juvenile hormones (JH). Temperature and photoperiod are involved in the activities of insect's endocrine glands, corpora allata that used to be the synthesis of JH (RESH and CARDÉ 2009). Therefore, low temperature and short daylight lead to shut down insect's endocrine glands, corpora allata and thereby, it might lead to a decrease in the production of eggs. This speculation is consistent with a previous study demonstrating that in *Bombus terrestris* (Linnaeus) (Hymenoptera: Apidae) the rates of JH biosynthesis are low during pre-diapause and diapause, and corpora allata reactivation occurs only several days after diapause termination (LARRERE et al.1993). Insulin signaling is suppressed under short daylight, which in turn suppresses juvenile hormone synthesis within the *corpora allata* (TATAR and YIN 2001, TU et al. 2005).

5.2. INBREEDING DEPRESSION AND ITS EFFECTS ON DIFFERENT LIFE TABLE PARAMETERS AND SEX RATIO

5.2.1. Effects of brother and sister inbreeding on longevity

There were significant differences in longevity of the L1 and T lineages under different brother and sister inbreeding generations F (2, 139); 31.491, P< 0.001 and F (2, 134); 38.79, P< 0.001), respectively. The inbred females of the L1 and T lineages lived significantly shorter in the F_2 and F_3 generations, as compared with longevity of those females in the F_1 generation. The longevity of both lineages were significantly lower in the F_3 generation than that of those females in the F_2 generation. There was 27 and 43 % longevity reduction for L1 lineage in the F_2 and F_3 generation, respectively, and it was 30 and 44 % for T lineaage in the F_2 and F_3 generations, respectively, as compared with the longevity of females in the F_1 generation. This indicates that continued brother and sister inbreeding increase the sufferity of inbreeding depression in longevity. The longevity of the T lineages was a little bit longer in all generations (**Figure** 11).

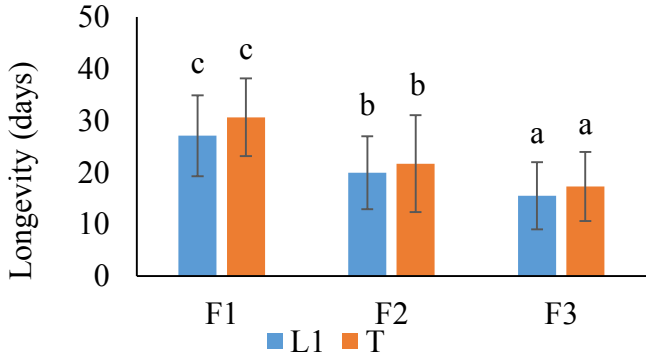

Figure 11: The comparison of brother and sister inbreeding on longevity at different generations. Where different letters are used to indicate significant difference with P<0.05, and similar letters are used to indicate non-significant difference between different generations with p>0.05.

5.2.2. Effects of brother and sister inbreeding on fecundity

The fecundity rates of the L1 and T lineages were significantly different under different brother and sister inbreeding generations (F (2,134); 39.142, P< 0.001), F (2, 139); 29.549, P< 0.001, respectively). In both lineages, fecundity reduction was started from F_2 generation and greately reduced in the F_3 generation. In both lineages, the inbred females laid 59 % fewer eggs in the F_3 generation than as compared with the inbred females in the F_2 generation. The fecundity of the T lineages was a little bit less in all generations. This indicates that subsequent brother and sister inbreeding induced higher depression on the fecundity of L1 and T lineages (**Figure** 12).

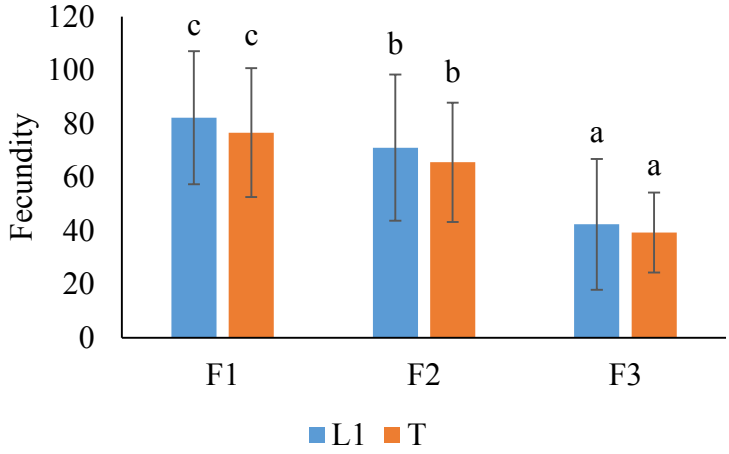

Figure 12: The comparison of brother and sister inbreeding on fecundity at different generations. Where different letters are used to indicate significant difference with P<0.05, and similar letters are used to indicate non-significant difference between different generations with p>0.05.

5.2.3. Effect of brother and sister inbreeding on egg hatchability

The egg hatchability rates of the L1 and T lineages were significantly different under different brother and sister inbreeding generations (F (2, 134); 69.299, P< 0.001), F (2, 139); 36.128, P< 0.001), respectively). Egg hatchability rate started to decrease from F_2 generation for both lineages. There were significant differences in egg hatchability rates between F_2 and F_3 for the L1 lineage but there was no significantly different inbreeding depression was detected for T lineage. In both lineages, more than 82% of eggs hatched in the F_2 generation, although the egg hatchability rates were less than 72 and 80 % in the F_3 generation for L1 and T lineages, respectively. The egg hatchability of the T lineages was significatly better in the F1 and F2 generations (**Figure** 13).

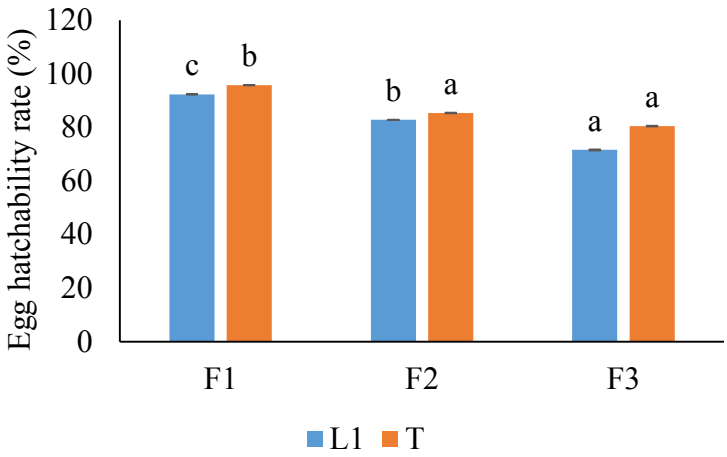

Figure 13: The comparison of brother and sister inbreeding on egg hatchability rate at different generations. Where different letters are used to indicate significant difference with P<0.05, and similar letters are used to indicate non-significant difference between different generations with p>0.05.

Inbreeding depression is more intense in diploid species than in haplodiploid species (HEDRICK and PARKER 1997, HENTER 2003). However, the incidence of inbreeding may not be different between haplodiploid and diploid organism: if there are genes that solely govern the traits of diploids, i.e. females limited genes (HENTER 2003). The variation in reproductive fitness is due to the level of selection of recessive deleterious alleles. Subsequent counter selection of deleterious recessive alleles in haploid males significantly reduces the genetic load and due to this, haplodiploid species carry less recessive deleterious alleles than diploid species (ROFF 2002, CHARLESWORTH and WILLIS 2009). Because the haploid male imposes purifying selection of recessive deleterious alleles and hence exposed to continuous selection which greatly decreases their frequency in the population (AVERY 1984, WERREN 1993). However, alleles of genes only expressed in the diploid females are protected against purifying selection in heterozygous individuals. This leads to the prediction that haplodiploidy suffers to inbreeding effects on life-history traits (SAITO et al. 2000).

In this result, brother and sister inbreeding of the L1 and T lineages caused greater longevity reduction. The negative effect of inbreeding on the longevity was expressed after a single round of inbreeding. High inbreeding effect on the longevity (38 % longevity reduction) has been reported in *Uscana semifumipennis* (Girault) (Hymenoptera: Trichogrammatidae) (HENTER 2003). We found that the effect of brother and sister inbreeding on longevity was the same among lineages and this indicates that the longevity of these two lineages are likely similar in their suscebtibility to inbreeding depression. As longevity is not a female trait only: it is surprising to detect sever inbreeding depression a trait is not obviously sex limited. HENTER (2003) reasoned out that it could be that longevity for males and females is under different genetic control. As the

inbreeding effect continued for third generation, the inbreeding depression may be due to over dominance. Because, when overdominance is the cause a continuously inbred line will never be as fit as an outcrossed line once variation is lost. Finally, it could be that haplodiploidy does not purge genetic load effectively enough to prevent inbreeding depression (HENTER 2003).

We tested the effects of brother and sister inbreeding on fecundity for three subsequent generations and the result has shown that the inbreeding depression detected since from F_2 generation. In this result, brother and sister inbreeding of the L1 and T lineages caused approximately 11 and 38 % fecundity reduction in the F_1 and F_2 generations, respectively. Thus, the magnitude of inbreeding depression between the two lineages seemed similar. The ovipositing inbred females in the L1 and T lineages were less likely to lay eggs in the F_2 and F_3 generations than outbred females in the F_1 generation. Life- time productivity show high levels of inbreeding depression in *Drosophila simulans* (Sturtevant) (Diptera: Drosophilidae) (WRIGHT et al. 2008). It is possibly less surprising to see inbreeding depression in fecundity, given that this is clearly a female trait. The fecundity reduction for inbred females in both lineages may be interlinked with the mating ability of inbred males. Mating with inbred males has significant direct effects for the fitness of female in the *Callosobruchus maculatus* (Fabricius) (Coleoptera: Chrysomelidae), likely mediated by effects of inbreeding status on the number of sperm in male ejaculates. Fecundity reduction due to the reduced number of sperm in the ejaculates of inbred males has been reported in the *C. maculatus* females (FOX et al. 2012). Inbreeding generally reduces male mating activity such that inbred males can also have smaller accessory glands, transfer less sperm and produce sperm that are less motile, less viable or have a greater frequency of abnormalities, all of which can reduce the fertilization success and fitness of inbred male's relative to outbred males (FOX et al. 2012). That inbred males produce fewer sperm and high levels of inbreeding reduce male fertilization success under sperm competition in guppies *Poecilia reticulate* (ZAJITSCHEK et al. 2009). The other possible reason may be related to the vulnerability to inbreeding depression and could thus mediate the male- specific effect of inbreeding. The negative effect of inbreeding known to affect spermatogenesis is to decrease the number of sperm in the ejaculates of inbred males in *Forficula auricularia* (Linnaeus) (Dermaptera: Forficulidae) and lead to reduce the number of eggs produced by the mating partners (FOX et al. 2011, OKADA et al. 2011). The other potential negative effects of inbreeding is to reduce the quality of sperm in the ejaculates of inbred males, which hampers embryonic development, lowers the hatching success of the eggs, as well as reduces the number of eggs that females are able to produce after having stored the sperm for a relatively long time (MEHLIS et al. 2012). The fecundity of female in *C. maculatus* was sperm limited, and this was primarily occured when females mate with inbred males (FOX et al. 2011).

The results of our study show that subsequent brother and sister mating led to decrease the egg hatchablity rate in the L1 and T lineages. The egg hatchability percentage in the L1 and T lineages started to decrease from the F_2 generation. Brother and sister inbreeding caused 11 and 23 % egg hatchability rate for L1 lineage in the F_2 and F_3 generations, respectively, and 11 and 26 % hatchability rate for T lineage in the F_2 and F_3 generations, respectively. These indicats that the inbred females in the L1 and T lineages were less likely to hatch in the F_1 and F_2 generations. The egg hatchability rates in the L1 were significantly different between F_2 and F_3 generations. However, there was no significant different in the T lineage between F_2 and F_3 generations. Sever inbreeding depression in egg hatchability rates have been reported in *Lymantria dispar* (Linnaeus) (Lepidoptera: Erebidae) (HIGASHIURA et al.1999).

5.2.4. Effect of brother and sister inbreeding on sex ratio of the progeny

The male: female ratios in the progeny of females of L1 and T lineages were significantly influenced by brother and sister inbreeding depression. In both lineages, there were significant differences in the male proportions between F_1 and F_3, and between F_2 and F_3, generations, and there was no significant difference in the F_2 generation compared with the F_3 generation. This indicates that in the F_1 generation, male ratio was notably higher than in F_2 and F_3 generations for both lineages, L1 and T (**Table** 16).

Table 16: The proportion of male and female progeny of *T. tabaci* lineages produced at different generations of brother and sister inbreeding (%)

Lineage	F_1	F_2	F_3
	Male: Female	Male: Female	Male: Female
L1	26.17b	21.37a	18.41a
T	26.01b	22.22a	20.27a

Notice: Different letters are used to indicate significant ($P < 0.05$) and similar letters are used to indicate non-significant difference between generations ($P > 0.05$).

In this study brother and sister, inbreeding has a direct effect on the variation of proportions of male and female. The proportion of male in both lineages was about 26 % in the F_1 generation, which is the expected proportion in the arrhenotokous thrips species (LEWIS 1973). However, the proportion of males in both lineages was significantly lower in the F_3 generation than in the F_1 and F_2 generations. Thus, frequent brother and sister mating led to female biased progeny in both lineages. In this treatment, brother and sister inbreeding negatively affected the lifetable

parameters of the inbred mothers, this indicates that the mothers were in poor condition and this may lead to female biased progeny at F_3 generation.

5.3. EFFECT OF TEMPERATURE ON SEX RATIO AND LIFETABLE PARAMETERS

5.3.1. Effect of temperature on preoviposition

The pre-oviposition periods of females of the L1 and T lineages were significantly influenced by temperature treatment ($F(2, 89) = 119.96$, $P<0.001$; ($F(2,116) = 138.11$, $P<0.001$, respectively). The pre-oviposition periods of L1 and T lineages were significantly longer with decreasing temperature settings. The preoviposition periods of L1 and T lineages at 15 °C were 5.5 and 8.5 times, respectively longer than those females reared at 30 °C (**Table** 17).

Table 17: The preoviposition period of *T. tabaci* lineages at different temperature (Mean±SD)

Lineage	Temperature (°C)		
	15	23	30
L1	5.47 ± 4.89^{c} (n=17)	2.08 ± 0.88^{b} (n=38)	1.00 ± 0.00^{a} (n=37)
T	11.31 ± 3.37^{c} (n=19)	1.89 ± 1.11^{b} (n=35)	1.31 ± 0.60^{a} (n=45)

Note: Different letters indicate a significant difference between different temperature levels (Games-Howell's, $p<0.05$).

The results from this experiment has shown that the mean preoviposition period of the L1 and T lineages was extended with decreasing temperature. FEKRAT et al. (2009) reported that the preoviposition period of the L1 and T lineages was 2.35 and 2.5 days at 25 °C on onion and tobacco, respectively. MURAI (2000) reported that the preoviposition period of the L2 lineage was 3.41 days at 23 °C on honey and pollen, which seems to be higher in comparison to the preoviposition period of the L1 and T lineages. SAKIMURA (1937) has reported that the preoviposition of the thelytokous *T. tabaci* lineage was 3.9 days at 15 °C on *Allium cepa*, which is relatively shorter as compared to our results and that of reported by MURAI (2000). In our study, females of the L1 and T lineages have a similar preoviposition period at 23 °C, but have a very different preoviposition period at 15 °C. MURAI (2000) has stated that the preoviposition period of the L2 lineage was 8.64 at 15 °C on honey and pollen, which is quite different to the preoviposition of the L1 lineage in this study. However, females of the T lineage in our study seem to have a relatively longer preoviposition period at 15 °C than females of the L2 lineage in the study of MURAI. In our study, the preoviposition period of the L1 and T lineages was equal and little longer, respectively than one day at 30 °C and it seems to be shorter than the preoviposition period (of the L2 lineage at 30 °C (1.96 days) on honey and pollen (MURAI 2000).

5.3.2. Effect of temperature on fecundity

The fecundity rates of the L1 and T lineages were significantly different under different temperature levels ($F(2, 89) = 27.12$, $P<0.001$; $F(2,116) = 7.71$; $P<0.01$, respectively). The lowest fecundity of the L1 lineage was recorded at 15°C, and significantly greater fecundity rates were observed at 23°C and 30°C, whereas the fecundity rates of the T lineage were not significantly different at 23°C and 15°C and it was significantly lower at 30°C than that of at 23°C (**Table** 18). This indicates that the responses of the two lineages to temperature are clearly distinguishable at 15°C. Reproductive diapause was detected for 29 and 7 females in the L1 and T lineage at 15°C, respectively. This indicates that the incidence of reproductive diapause is higher in the L1 lineage at 15°C.

Table 18: The fecundity of *T. tabaci* lineages at different temperature (Mean±SD)

Lineage	Temperature (°C)		
	15	23	30
L1	19.88 ± 12.65^{a} (n=17)	107.63 ± 74.15^{b} (n=38)	74.78 ± 29.47^{b} (37)
T	70.82 ± 38.48^{ab} (n=39)	84.83 ± 28.57^{b} (n=35)	58.33 ± 21.40^{a} (n=45

Note: Different letters indicate a significant difference between different temperature levels (Games-Howell's, $p<0.05$).

Our results indicate that among the tested temperature levels 23 °C is the optimal temperature for the reproduction and egg laying of *T. tabaci* lineages. MURAI (2000) has reported that the fecundity of the L2 lineage was 270 eggs at 23 °C on honey and pollen, however, the fecundity started to decrease at 25°C and dropped drastically to 62 eggs per female at 30°C. Thus, food source also affects lifetable parameters of *T. tabaci* (MORAIET et al. 2017). VAN RIJN et al. (1995) reported that females of *T. tabaci* produced 27.5 eggs on cucumber at 25°C. HASSANZADEH et al. (2003) reported on onion plants at 27°C an average of 31.63 eggs. SAKIMURA (1937) presented also that *T. tabaci* deposited 80 eggs on *Allium cepa* at 18°C. In our study, the fecundity of the L1 lineage was significantly decreased at 15 °C than at the other two temperature levels, but the fecundity of the T lineage at 15°C was statistically non-significant difference to that of at 23 °C, which indicates that the T lineage could better tolerate lower temperatures than the L1. The fecundity reduction was observed for both lineages at 30°C and it seems to be close to the upper threshold in the entire *T. tabaci* cryptic species complex.

5.3.3. Effect of temperature on egg hatchability

The egg hatchability rates of the L1 and T lineages were significantly different under different temperature levels ($F(2,89) = 34.87$, $P<0.001$; $F(2,116) = 22.19$, $P<0.001$, respectively). It revealed that there were significant differences in egg hatchability rates under 15°C and 30 °C for the L1 lineage but no significantly differences under 15 and 23°C. The egg hatchability rates were pairwisely significantly different under 15, 23 and 30°C for the T lineage. The egg hatchability rates for both lineages were significantly higher at 15°C and 23°C than at 30°C. In both lineages, more than 85% of eggs hatched at 15°C and 23°C, while the rates were less than 78% at 30°C (**Table** 19).

Table 19: The egg hatchability of *T. tabaci* lineages at different temperature (Mean±SD)

Lineage	Temperature (°C)		
	15	23	30
L1	93.05 ± 7.16^{b} (n=17)	95.28 ± 7.67^{b} (n=38)	78.13 ± 14.22^{a} (n=37)
T	91.26 ± 9.65^{c} (n=39)	86.71 ± 6.16^{b} (n=35)	76.13 ± 14.12^{a} (n=45)

Note: Different letters indicate a significant difference between different temperature levels (Games-Howell's, $p<0.05$).

In both lineages 76-78% of the eggs hatched at 30 °C and about 91-93% of the eggs hatched at 15 °C and 86-95 % of the eggs hatched 23 °C. This suggests that high temperature is likely to have a direct effect on the egg hatchability rate. MURAI (2000) has reported that only 10% of the eggs hatched in L2 lineage at 30 °C, which is an extremely high percentage of egg mortality as compared to our study. However, in our result the egg hatchability of L1 and T lineages is mild drop at 30°C, while the egg hatchability of the L2 was drastically dropped at 30 °C (MURAI 2000). Thus, the L1 and T lineages fares better at 30 °C than L2 lineage. Therefore, it suggests that L1 and T *T. tabaci* lineages have a better capacity to survive at high temperature as that of the L2 lineage. JIANG et al. (2016) reported that 100 % egg mortality of *A. obscurus* was observed at 35 °C. SAKIMURA (1937) reported a summer decline in the density of Japanes population of *T. tabaci*, a trend that may be indicated by the high egg mortality at high temperatures. (EKESI et al. 1999) described that the population of *M. sjostedti* decreased at 30 °C due to less fecundity and high egg mortality rate.

5.3.4. Effect of temperature on longevity

There were significant differences in longevity of the L1 and T lineages at different temperature levels ($F(2, 120) = 47.13$, $P<0.001$; $F(2,120) = 529.56$, $P<0.001$, respectively).

Longevity of the L1 and T lineages decreased log-linearly significantly with raised temperature conditions (R=-0.64; P<0.001; R=-0.90; P<0.001, respectively). Maximum longevities of the T lineage was more than two times longer as in the L1 lineage (**Table** 20).

Table 20: The longevity of *T. tabaci* lineages at different temperature (Mean±SD)

Lineage	Temperature (°C)		
	15	23	30
L1	34.22±9.88^{c} (n=46)	24.64±12.28^{b} (n=39)	13.63±5.45^{a} (n=38)
T	81.82±15.26^{c} (n=45)	26.20±5.27^{b} (n=35)	13.91±3.88^{a} (n=43)

Note: Different letters indicate a significant difference between different temperature levels (Tukey's, p<0.05).

Adult longevity significantly affected by temperature and was the shortest at the upper temperature (30 °C) for L1 and T lineages. MURAI (2000) also reported a decrease in the longevity of L2 lineage as temperature increases (12.8 days), which means the effect of higher temperature on longevity is similar in the entire *T. tabaci* cryptic species complex. TEULON and PENMAN (1991) also presented a decrease in longevity of *T. obscuratus* as temperature increases. This result suggests that the temperature at 30 °C have an inhibitory effect on the longevity of the L1 and T lineages. There were 24 females of the T lineage at 15 °C that produced only male offspring and they were considered as virgin females. Although, in contrast, mated or virgin females did not differ in probability of longevity. Therefore, mating at 15 °C does not have a significant effect on longevity, which is also known from L1 lineage at 20 °C (LI et al. 2015), *Franklinothrips* n. sp. at 20 and 25 °C (HODDLE et al. 2000), and *E. americanus* at 23 °C (KRUEGER et al. 2016a). In our experiment the longer longevity of the L1 and T lineages were observed at 15 °C (34.22 and 81.82 days), respectively, which means that T lineage fares better at low temperature than L1 lineage.

5.3.5. Effects of temperature on the sex ratio

The number of larvae identified as male and female from each temperature treatments are presented in Table 21. The male: female ratios in the progeny of females of the L1 and T lineages were significantly influenced by temperature treatment ($F(2, 91) = 12.48$, $P<0.001$; $F(2, 91) = 6.47$, $P<0.01$), respectively. In both lineages, there were significant differences in the male and female ratio between conditions under 15°C and 23°C, and between the ones under 15°C and 30°C, and there was no significant difference in male and female ratios compared conditions under 23°C and 30°C. The proportion of males log-linearly decreased as temperature increased (R=-0.40; P<0.001;

R=-0.34; P<0.001, respectively), and the proportion of females decreased as temperature decreased. This shows that under 15°C, male ratio was notably higher than under warmer conditions for both lineages, L1 and T (**Table** 22). All females of the L1 lineage were successfully mated (females produced both male and female progenies), while 24 females of the T lineage were not successfully mated (females produced only male progenies) at 15°C.

Table 21: The number of larvae slide mounted to identify their sex

Lineages	Temperature (°C)					
	15		23		30	
	Male	Female	Male	Female	Male	Female
L1	113	151	975	2969	376	1822
T	510	821	616	1793	419	1561

Table 22: The proportion of male and female progeny of *T. tabaci* lineages produced at different temperature levels

Lineage	Temperature (°C)		
	15	23	30
	Male: Female	Male: Female	Male: Female
L1	0.98 ± 73.18^{b} (n=17)	0.42 ± 71.15^{a} (n=39)	0.29 ± 30.60^{a} (n=38)
T	0.86 ± 84.08^{b} (n=15)	0.42 ± 33.15^{a} (n=34)	0.42 ± 57.74^{a} (n=45)

Note: Different letters indicate a significant difference between different temperature levels (Tukey's, p<0.05).

Temperature has a direct effect on the variation of proportions of male and female. In our study, the proportion of females in both lineages was significantly less at 15 °C and higher at 30 °C. The sex ratio (female/male) of *Thrips palmi* (Karny) (Thysanoptera: Thripidae) adults on eggplant was highest (2.03) at 31° C and the lowest (1.22) at 16° C (YADAV and CHANG 2014). The observed natural proportion of males of the arrhenotokous *T. tabaci* lineage was highest in June until the beginning of July and was subsequently decreasing in summer becoming the lowest at the end of August on potato (JENSER et al. 2006). Nevertheless, in the warm climate of Iran, *T. tabaci* has the sex ratio 1:1, and much lower ratios have been recorded on the colder, parts of the world (OLSEN 1984). Producing significantly higher proportion of females at 23 and 30°C reveals that the arrhenotokous *T. tabaci* lineages can easly build-up its population, while producing

significantly lower proportion of females at 15 °C reveals that the arrhenotokous *T. tabaci* lineages can slowly build-up its population.

There seems to be geographical variation in the presence of males in different populations of the same species. *T. tabaci* is cosmopolitan, but males are absent or rare throughout much of its geographical range. KENDALL and CAPINERA (1990) has reported that the worldwide distribution of the proportion of males is highly correlated with longitude and the majority of arrhenotokous populations occurs in the western hemisphere.

5.4. THE EXISTENCE OF DEUTEROTOKOUS REPRODUCTION MODE

5.4.1 Pupal insemination

In this result, adult males have attempted to mate with female pupa, but pupal insemination is not possible in the *T. tabaci* lineages within 24 hours of mating. Thus, all the tested females produced only male progeny (N=988) in the arrhenotokous leek-(L1) and tobacco associated- (T) *T. tabaci* lineages (**Table** 23).

Table 23: The sex of progeny produced from virgin L1 and T type females that were exposed to male adult at pupal stage

Lineages	First instar male	Second instar male	Pupae progeny	Adult male progeny	Total male
L1	187	95	66	118	466
T	252	121	22	127	522

There are feasible reasons to explain the failure of female pupa to inseminate by an adult male: such as (1) this stage is inactive and could not identify the sex hormone produced by the male to mate. (2) the developmental stages of *T. tabaci* are passed through moulting and adult male genital might not get the female pupa genital part; because the moult skin might cover the female pupa reproductive part. (3) The pupal stage of *T. tabaci* is inactive for feeding and at the same time, the reproductive part might not be well developed.

5.4.2. Mother to son inbreeding

Deuterotokous reproductive mode was detected in the T lineage during mother to son inbreeding test. At F_2 generation, the inbred virgin female of T lineage taken from F_1 generation produced a combination of male and female progenies, and this female was considered as a deuterotoky ones (**Table** 24).

Three virgin females of T lineage produced a total of 20 females and 75 males in two consecutive generations (Table 25). F_{1D} female has produced 10 deuterotoky females, and 2 of them died at the pupal stage; of the 8 deuterotoky females, only 1 female was continued to produce both males and females and the rest 7 females were turned to their original arrhenotokous mode of reproduction. Similarly, at F_{2D} generation, of the eight deuterotoky females, only one virgin female yielded both male and female progenies and the rest seven females were turned to their original arrhenotokous reproduction mode. After three generations, all the deuterotoky females turned to their original arrhenotokous mode of reproduction.

Table 24: The existence of deuterotokous mode of reproduction

Generation	No. of female	Male	Female	Reproduction mode	Deutero-toky mother
F_1	30	✓	X	Arrhenotoky	0
F_2	17	✓	✓	Deuterotoky	1/17

Table 25*:* A sex ratio of progeny that were produced by deuterotoky virgin female for three consecutive generation

Generation	No. of deuterotoky female	No. of progeny from deuterotoky female		Reproductive mode
		Male	Female	
F_{0D}[a]	1	5	8	Deuterotokous
F_{1D}[b]	1/8	4	10	Deuterotokous
F_{2D}[c]	1/8	66	2	Deuterotokous
F_{3D}[d]	2	72	0	Arrhenotokous

[a]F_{0D} the deuterotoky female produced from F_2 inbred mother; [b]F_{1D} – the deuterotoky female progeny produced from F_{0D} female; [c]F_{2D} – the deuterotoky female progeny produced from F_{1D} female; [d]F_{3D}, the female produced from F_{2D} female

All modes of reproduction have been reported in *T. tabaci* populations. However, deuterotoky is relatively uncommon mode of reproduction in *T.tabaci* because it has been reported only by NAULT ET AL. (2006) and it still might be thought of as mere developmental irregularities. Such a scenario was led to our research. This reproductive irregularitiy might be raised due to mating between relatives, which, led to induce depression effects on the next generation.

Our result has shown that mother and son inbreeding has induced deuterotokous reproductive mode in the T lineage (the virgin inbred female produced the combination of male and female progeny). Therefore, the mating between mother and son potentially changes the

arrhenotoky female to deuterotokous reproductive mode in the T lineage. However, deuterotokous reproduction mode was not detected in the L1 mother and son inbreeding for the tested generations. The deuterotokous females of T were reared for three subsequent generations, their progeny sex ratio was female biased at F_{0D}, and F_{1D} generations and during the F_{2D} generation the proportion of males were higher than females. Lastly, the deuterotokous females turned back to their original arrhenotokous reproduction mode. F_{3D} deuterotokous females produced all male progeny. Therefore, this result indicated that deuterotokous reproductive mode is not a persistence reproductive mode in the T type other than it is irregularity reproductive mode.

Reproductive mode determination in *T. tabaci* lineage based on the sex of progeny takes more time. A time saving technique for differentiation of the reproductive mode using the COI sequences was reported (TODA and MURAI 2007). However, sometimes the lineages showing arrhenotokous were reported wrongly as showing thelytoky according to the COI based technique (AIZAWA et al. 2016). This might be due to the interbreeding between arrhenotokous and thelytokous *T. tabaci* lineages is resulting the thelytokous female carry arrhenotokous male-originated nuclear gene (LI et al. 2015). Heteroplasmy where females carry multiple mitochondrial DNA genes within the cell has been reported in *T. tabaci* population (GAWANDE et al. 2017).

Deuterotoky females detected in the T lineage due to mother and son inbreeding, but not in the L1 lineage. Since deuterotoky females has been reported in the L1 lineage, The reason that we did not find in the mother and son inbreeding would be due to less replication, or this might be due to the susceptibility rate differences of inbreeding depression between the two lineages. Variation in the detection of deuterotoky due to mother and son inbreeding might be one of the biological differences among the L1 and T lineages.

5.5. FIGHTING BEHAVIOUR OF MALE IN *T. TABACI* LINEAGES

5.5.1. Behavioural observations during fighting

Aggressive fighting interactions of *T. tabaci* males occurred in the small arena with different fighting movements. When the two contestants approached each other, they first contacted each other with their moveable antennae, and then chased each other around the arena. Occasionally, the contestants stopped to vibrate their wings and rub their hind legs. Antennal bouts (**Figure** 14a), jumping (**Figure** 14b) flipping, stabbing and pitching (**Figure** 15c) are the most commonly observed fighting movements. Fights often ranged from few initial abdominal bouts, antennal flicking to escalated aggressive interactions. Several prolonged fights with stabbing and pitching beyond the less aggressive abdominal and antennal bouts, abdominal flipping and flicking, were observed.

In this experiment, similar fighting movements were observed in the L1 and T males: (1) Parallel abdominal bouts: the males lining up in side-to-side and flicking abdomens at each other. (2) Antennal bouts: the males approached each other and rapidly vibrated their antennae up and down until they made antennal contact. The antennal contacts ranged from a rhythmic, but calm movement to rapid movements. (3) Stabbing and pitching: where one male climbed onto the back of the other male and grasped the contestant with its forelegs. (4) Flipping: where a male quickly lifted its abdomen directly into the air. Flipping of the abdomen may be used as a defensive strategy. (5) Jumping: where both males lifted their thorax, and flipped forelegs toward the head of their opponent to grasp each other.

Figure 14: The most frequent fighting movements observed between T. tabaci males of L1 and T lineages of the onion thrips in a laboratory experiment: (a) antennal bouts, (b) jumping, and (c) stabbing and pitching fighting tactics.

5.5.2. Fighting performance

The video recordings showed that while all tested L1 males fought and had more aggressive interactions, only half of the tested T males fought (**Figure** 15).

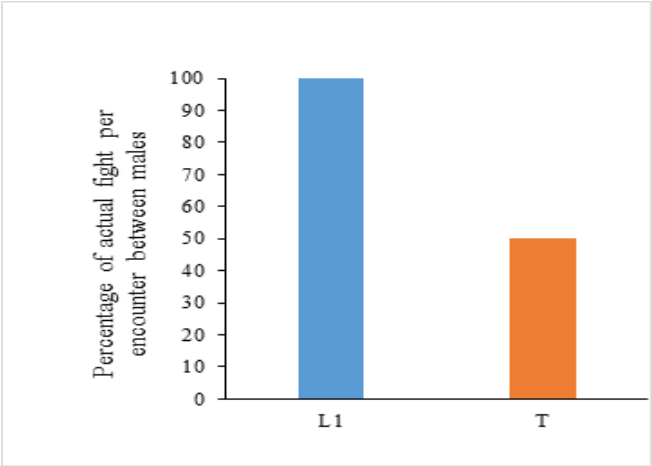

Figure 15: Comparison of actual fights per encounter between males of L1 and T lineages of the onion thrips in a laboratory experiment.

5.5.3. Fighting frequency, pre-fight period, duration of fight and refighting time interval

No significant differences were found in the fighting frequencies, pre-fight periods, durations of fights and refighting time intervals. F (1: 22) = 4.049; P>0.05, F (1:22) =1.861;

P>0.05, F (1, 22) =3.296; P> 0.05, F (1, 22) = 0.046; P> 0.05 (**Table** 27). Fights between males of T lineage were less frequent and calmer. Duration of fight was longer between members of the L1 lineage than those of the T lineage, while the prefight period and refight time interval was longer between members of the T lineage than those of L1 lineage (**Table** 26). L1 males have shown immediate mobility to fight, and were more active throughout the experiment.

Table 26: The rate of fighting interactions between L1 and T males

	L1	T
Fighting frequency	4.25 ± 2.7 a	2.45 ± 3.24 a
Pre-fight period (sec)	84.90± 167.05 a	191.91 ± 213.61 a
Duration of fight (sec)	7.45 ± 8.05 a	3.55 ± 2.62 a
Refighting time interval (sec)	120.00 ± 120.58 a	193.73 ± 207.63 a

Where: Similar lower-case letters indicate no significant difference (p> 0.05).

Aggressive fighting interactions occurred in the small arena with different fighting movements. Parallel abdominal bouts, antennal bouts, flipping, stabbing, and jumping were the most frequent fighting movements in both L1 and T lineages. These movements can be considered assessments: this is how an individual may determine the body size and fighting ability of its opponent to decide whether to continue or stop fighting. SMITH (1982) found that assessment occurs when the success of a future fight between opponents is perceived low in the first phase of the interaction. Assessments usually settle the fights without escalation. Assessments of fighting abilities between the opponents were reported in *E. tuberculatus* and *Hoplothrips karnyi* (CRESPI 1988a). *E. tuberculatus* males assess the size of their opponent in two stages: during the initial approach and the initial parallel bout. The outcomes of assessments between males in fights is that the greater male chases the smaller one until it flees rather than being engaged in the fight (CRESPI 1986a). For the decision to flee, insects are thought to assess information from agonistic signals exchanged during the fighting (STEVENSON and RILLICH 2012). Individuals of certain insect species assess their own fighting ability, and not that of their opponent. This is the case in honeybees (DIETEMANN et al. 2008). Self-assessment can occur during a contest, and an individual may decide to retreat when the costs imposed by the opponent reaches a certain threshold (TAYLOR and ELWOOD 2003). Therefore, self-assessment during the fight may inform the individual that his opponent is weak and does not represent a threat to the resource.

Indeed, for weak contestants that do not have information about the fighting ability of their opponents, the highest survival chance is given by not initiating a contest (PAYNE 1998).

Fighting causes a lethal effect in *H. karnyi, K. rugosus*, *O. tepperi*, *Koptothrips flavicornis and E. tuberculatus* (CRESPI 1986a, 1988a, 1988b, 1992,). Lethal fighting occurs between contestant's due to the presence of enlarged forelegs, and large fore tarsal claws, which both give individuals an advantage over their less well-endowed opponents (MOUND 1991). Those physical structures are much smaller in members of the Terebrantia thrips species than in members of the Tubulifera thrips species. Although there were no immediate lethal fights in L1 and T lineages, fighting may cause long-run risks for their total longevity. Fighting males also lose time and energy that might be used searching for females (TERRY 1995). In our experiment, both lineages showed different fighting performance. L1 males exhibited more frequent fighting as 100 % of them fought, whereas T males fight less frequently. By contrast, the L1 males had a longer duration of fight, shorter prefight period, and refighting interval than T males. The difference between fighting in the two lineages is likely due to the variation in type and quantity of male-produced pheromones. Males interact over extended periods, so a pheromone may be involved as were found with males of sandfly, *F. occidentalis*, *F. intonsa*, *M. sjostedti* and *T. palmi* (JONES and HAMILTON 1998, HAMILTON et al. 2005, ZHANG et al. 2011, AKELLA et al. 2014, KIRK 2017, NIASSY et al. 2019). It has been reported that a male *F. occidentalis* produces pheromone during aggregation. Furthermore, it has been noted in the Australian field cricket that male dominance status is associated with the expression of male pheromone signals (THOMAS and SIMMONS 2009). AKINYEMI and KIRK (2019) found that an antiaphrodisiac pheromone was produced in *F. occidentalis* males but not in females. Thus, as L1 and T lineages have substantial variations genetically and in host adaptations, the type and quantity of male-produced pheromones may be varied too, and it may be the reason behind variations in the intensity of male fighting performance observed.

In addition, the reason behind the different fighting behaviours of the two lineages might be the body size difference between the fighter and non-fighter males in these lineages. TERRY and DYRESON (1996) observed that in *F. occidentalis* males with wider abdomens and larger legs tend to be more aggressive during fighting and frequently engage in fights. These authors explain that a stouter abdomen gives more torque for offensive movements (such as flicking the opponent) and increased momentum of inertia for defensive movements. In addition, larger legs increase the ability to grab the opponent.

It is not clear what males gain from fighting in the absence of females and food in the arena. TERRY and GARDNER (1990) suggested that males might be defending a space. Males with

proportionately larger weaponry initiate fights in *Gryllus pennsylvanicus* (Burmeister) (JUDGE and BONANNO 2008). Large males of the dew drop spider, *Argyrodes antipodiana* are more likely to induce fight than small males of the same species (WHITEHOUSE, 1997). It is possible that chemical signalling controls fighting. Male-specific cuticular hydrocarbons and male-produced pheromones play a vital role in communication, particularly in mating and fighting. However, these chemicals have not been studied in *T. tabaci* lineages. These two lineages have shown different fighting performances, and it might be due to their body size differences. Thus, the body size, type and amount of male-specific cuticular hydrocarbons and male-produced aggregation pheromones in L1 and T lineages need further studies.

6. CONCLUSIONS AND RECOMMENDATIONS

1. Reproductive diapause was detected in the T lineage due to 8L: 16D at 23 °C, and in the L1, L2, and T lineages due to lower (15 °C) temperature under 8L: 16D. Short daylight and low temperature affect the lifetable parameters of all three lineages.
2. Inbreeding between brother and sister caused inbreeding depression in the L1 and T lineages. Inbreeding depression was exhibitted on the longevity, fecundity, egg hatchability rate and sex ratio of the inbred females. The effect of mother and son inbreeding on the lifetable parameters of *T. tabaci* would be one of the study area.
3. The proportion of female increased as temperature increased and decreased as temperature decreased. The successfully mated L1 females produced a sex ratio (male :female) of 42.8 % and 57.2 % at 15 °C, 24.7 % and 75.3 % at 23 °C, 17 % and 83 % at 30°C; the mated T females 38.3 % and 61.7 % at 15 °C, 25.6 % and 74.4 % at 23 °C and 21 and 79 % at 30 °C . We can confirm that the offspring sex ratio of the females in both lineages are temperature dependent.
4. Pupal insemination is not possible in the L1 and T lineages.
5. Mother and son inbreeding induced deuterotokous reproductive mode in the T lineage. The role of brother and sister inbreeding for the existence of deuterotokous reproductive mode would eb a future studies area.
6. Fighting interactions were observed between the males in L1 and T lineages. The fighting was characterized by parallel abdominal bouts, antennal bouts, flipping, stabbing, and jumping fighting tactics. (1) Parallel abdominal bouts, (2) Antennal (3) Stabbing and pitching, (4) Flipping, and (5) Jumping. Fighting between males of the lineages in the absence of females and food in the arena, could be due to chemical signinals produced by males or to keep the territory. The two lineages showed different fighting performances, and it might be due to their body size differences. Thus, the body size, type and amount of male-specific cuticular hydrocarbons and male-produced aggregation pheromones in L1 and T lineages need further studies.

7. NEW SCIENTIFIC RESULTS

1. Reproductive diapause was detected in T lineage due to 8L: 16D at 23 °C and in all three lineages due to lower (15 °C) under 8L: 16D.
2. The subsequent mating between brother and sister caused inbreeding depression: the longevity, fecundity, egg hatchability rate of the inbred females were decreased in the L1 and T lineages.
3. The proportion of male decreased during subsequent brother and sister inbreeding. The successfully mated females with their brother produced notably higher female progeny in the F_2 and F_3 generations than F_1 generation.
4. The proportion of female increased as temperature increased and decreased as temperature decreased. The proportion of female increased as temperature increased and decreased as temperature decreased.
5. Pupal insemination is not possible in the *T. tabaci* lineages.
6. Mother and son inbreeding has induced deuterotokous reproductive mode in the T lineage.
7. Fighting interactions (parallel abdominal bouts, antennal bouts, flipping, stabbing, and jumping fighting tactics) were observed between the males in L1 and T lineages.

8. SUMMARY

Of the 6000 currently, identified thrips species (Thysanoptera), only about 1% is recorded as economically important pests. This figure has implied that Thysanoptera species cause major problem in agriculture. *Thrips tabaci* is among one of the major polyphagous thrips species since it has been recorded on more than 300 plant species. Therefore, its control is important to the production and profitability of crops.

The genetic variability of onion thrips has confirmed that *T. tabaci* is not a single pest species but rather a cryptic species complex. This concept is based on significant differences between the lineages regarding reproductive mode, host plant preferences and that there is considerable genetic variability within the three main lineages. The currently recognized lineages are arrhenotokous leek- (L1), thelytokous leek- (L2) and arrhenotokous tobacco-associated (T) lineages.

The results of the present study are summarized as follows:

Short daylight and low temperature levels affect the lifetable parameters of *T. tabaci* lineages. Reproductive diapause was detected due to short daylight alone in the T lineage and low temperature in all three *T. tabaci* lineages.

Brother and sister inbreeding affect the lifetable parameters of females in the L1 and T lineages. Subsequent mating between brother and sister caused inbreeding depression, which had a serious declining effect on the reproductive fitness of the next generation. Brother and sister inbreeding depression effects observed on longevity, fecundity, egg hatchability rate and sex ratio of the inbred females. The proportion of male decreased during subsequent brother and sister inbreeding.The successfully mated females with their brother produced notably higher female progeny in the F 2 and F 3 generations than F 1 generation.

The lifetable parameters of female in the *T. tabaci* lineages was strongly interlinked with temperature and showed a linear relationship between preoviposition, fecundity, egg hatchability, and longevity, throughout different temperature leveles. Higher or lower temperature ranges subsequently reduces the reproductive fitness of thrips species. Therefore, only species that can adapt quickly and efficiently to temperature change can survive. The proportion of female increased as temperature increased and decreased as temperature decreased. The proportion of female increased as temperature increased and decreased as temperature decreased. The successfully mated L1 females produced a sex ratio (male :female) of 42.8 % and 57.2 % at 15 °C, 24.7 % and 75.3 % at 23 °C, 17 % and 83 % at 30°C; the mated T females 38.3 % and 61.7 % at

15 °C, 25.6 % and 74.4 % at 23 °C and 21 and 79 % at 30 °C . We can confirm that the offspring sex ratio of the females in both lineages are temperature dependent.

The adult males have attempted to mate with the female pupae. However, the mating was not successful, consequently only male progeny was produced by all the tested progenies (N=988) in the arrhenotokous leek-(L1) and tobacco associated- (T) *T. tabaci* lineages. Pupal insemination was the suspected factor. However, this result has shown that insemination at pupal stage is not possible in *T. tabaci* lineages.

Mother and son inbreeding has induced deuterotokous reproductive mode in the T lineage (the virgin inbred female produced the combination of male and female progeny). Therefore, the mating between mother and son potentially changes the arrhenotoky female to deuterotokous reproductive mode in the T lineage. The deuterotokous females of T were reared for three subsequent generations, their progeny sex ratio was female biased at F_{0D}, and F_{1D} generations and during the F_{2D} generation the proportion of males were higher than females. Lastly, the deuterotokous females turned back to their original arrhenotokous reproduction mode, and thus, F_{3D} females produced all male progeny. Inbreeding between brother and sister might be induced the deuterotokous reproductive mode and it must be examined in the future studies

Fighting was observed between the males in the L1 and T lineages. The fighting was characterized by parallel abdominal bouts, antennal bouts, flipping, stabbing, and jumping fighting tactics. (1) Parallel abdominal bouts where two males line up side-to-side and hit at each other with their abdomens. (2) Antennal bouts where the males approached towards heads and rapidly moved their antennae up and down until they made antennal contact. The antennal contacts ranged from antenna rhythmic calm movement to frequently antenna rhythmic movement. (2) Stabbing and pitching where a male climb onto the opponent's back to grasp and squeeze the opponents with forelegs. (3) Flipping where a male quickly lifting up abdomens directly into the air. It may used as a defensive strategy. (4) Jumping where both opponents lifting up their thorax and flip forelegs towards the opponent's head to grasp each other. These may be used as an assessment of the opponent’s body size and fighting ability to decide either they can continue or withdraw fighting.

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