Chapter

Tuta absoluta (Meyrick) (Lepidoptera: Gelechiidae): An Invasive Insect Pest Threatening the World Tomato Production

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Abstract

The South American tomato pinworm or tomato leaf miner (TLM), *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), is a serious invasive and destructive insect pest of tomato (*Solanum lycopersicum* L.) worldwide. The moth can cause 100% damage in tomato crop in both greenhouses and open fields if control measures are not carried out. Due to the high reproduction potential, dispersal ability, and tolerance to environmental conditions, the TLM invaded most tomato-producing countries in Europe, Africa, and Asia. The tomato leaf miner originated in South America and was first introduced in Spain in 2006 and from where it spread to other part of the world. This chapter consolidates the rich literature on the pest with emphasis on invasion history, economic significance, and possible management options adopted worldwide.

Keywords: tomato leafminer, *Solanum lycopersicum*, invasive potential, management, Gelechiidae, quarantine pest

1. Introduction

Biological invasion has occurred for millennia, but increased globalization in recent decades has accelerated it [1]. Invasive insect species reduce crop yield, increase cost of production especially pest control costs, increase reliance on pesticides, and disrupt preexisting integrated pest management (IPM) programs. Invasive insect species cause considerable damage to agriculture, horticulture, and forest industries worldwide [2, 3] with an estimated annual economic loss of about 70 billion US$ [4]. Transportation and international trade are increasing rapidly, thus facilitating the spread and dispersal of invasive species [5]. The tomato (*Solanum lycopersicum* L.) is an important horticultural vegetable crop that is only second to potato. The total world production of tomato is about 180 million tons grown in areas of approximately 4 M ha. The top 10 tomato-producing countries in the world are China, India, USA, Turkey, Egypt, Italy, Iran, Spain, Brazil, and Mexico. China, India, and Turkey, account for almost half of the land area covered worldwide with tomato crops, that is, 31, 11, and 7%, respectively [6]. Tomato is the sixth most valuable cultivated crop in the world worth US$ 87.9 billion in 2016. The tomato leaf miner *Tuta absoluta* (Lepidoptera: Gelechiidae) is threatening about 87% of this production worldwide [3, 6, 7]. *T. absoluta* has several common English names in the literature. These are the South American tomato pinworm, the South American tomato leaf miner, the South American tomato moth, the tomato pinworm, the tomato borer, and the tomato leaf miner. For consistency, the tomato leaf miner (TLM) will be used throughout this chapter. The TLM has been considered as a key pest of tomato, in recent years, causing a reduction in tomato yield that can reach 100% if no management action is taken [1]. Increasing of global trade of tomato in the absence of strict quarantine measures and proper surveillance in many tomato-producing countries are the reason behind the vast spread of this pest.

Due to the significance of TLM, the Journal of Pest Science has recently published a special issue on this pest, which was edited by Biondi and Desneux [5]. The special issue gave more consolidated and updated information on the moth biology, population dynamics, chemical and trophic ecology, and novel control technologies. This chapter gives concise information on *T. absoluta* biology and bionomics, economic significance, geographical distribution, invasive potential, natural enemies, and available management options.

2. Origin, morphology, and taxonomic position

T. absoluta originated in the Peruvian Central highlands from where it spread to other areas of Peru and then to the rest of Latin American countries during the 1960s [3]. TLM is small moth with body length of 5–7 mm and wingspan of 10–14 mm [8]. The moth has silvery-gray scales and black spots on the forewings. The antennae are long, filiform with black and brown scales (**Figure 1**). Shashank et al. [9] described the male and female genitalia as well as the pupal genital aperture as useful distinguishing character for sexing of the moth. Egg is small (0.36 mm long and 0.22 mm wide) with elliptical shape and creamy white to bright yellow color. Larva is whitish in first instar (0.9 mm long) and becomes greenish or light pink in the second and fourth instar (7.5 mm). Pupa is obtect with greenish coloration at first, turning to chestnut brown and dark brown near adult emergence [8] (**Figure 2**). Tabuloc et al. [10] studies the genome of *T. absoluta* to generate and design a panel of 21 SNP markers for the species identification instead of depending only on morphological identification and symptoms of damage on the host plants.

Tuta absoluta was originally described as *Phthorimaea absoluta* (Meyrick, 1917) in Peruvian Andes. The genus was changed to *Gnorimoschema* [11] and then to Scrobipalpula [12] and Scrobipalpuloides [13]. Povolny [14] corrected the currently

Figure 1.
Adult moth of tomato leafminer, Tuta absoluta (photo: Antonio Biondi).

Figure 2.
Larva (top) and pupa (bottom) of Tuta absoluta (photo: Antonio Biondi).

used name *Tuta absoluta*. The EPPO code and phytosanitary categorization for *T. absoluta* are GNORAB and EPP A1 action list no. 321, respectively [8].

3. Biology and bionomics

The TLM has a complete metamorphosis type of reproduction, where it undergoes through four developmental stages, namely, egg, larva, pupa, and adult (**Figure 3**). Adults are nocturnal and hide between host leaves during the day. The female starts to release a sex pheromone 1–2 days after emergence to lure males for mating. The female sex pheromone is a mixture of tetradecatrienyl acetate and tetradecadienyl acetate in a ratio of 10:1, respectively [15, 16]. TLM is known to have multiple mating and the average number of mating per female is about 10.4. Both sexes are polygamous with no refractory period. The female sometimes can exhibit deuterotoky parthenogenesis, which gives both females and males from unfertilized eggs [17]. Males use female sex pheromone to locate females and mating can last from few minutes to 6 hours. Female uses plant volatiles (kairomones) and leaf contact for oviposition. A single female can lay as many as 260 eggs during its life cycle, which may extend to 3 months [18]. About 92% of the total eggs are laid in the 1–3 days following mating [8]. Eggs are laid singly on the upper part of the plant (young leaves, stems, and sepals). The eggs hatch in 5–7 days depending on temperature and relative humidity. After hatching, the larvae go through four instars, which are completed in about 20 days. The mature larva then gets rid of all gut materials, constructs a silken cocoon, and turns into pre-pupa and pupa. Pupation may last for 10–11 days before adult emergence for female and male, respectively. Mature larvae leave the mines and build silken cocoon on the leaflet or in the soil. When pupation occurs in the mines or tomato fruit, the pre-pupa does not build cocoon. Adult longevity may extend for 30–40 days [8]. The whole life cycle of the moth is completed in 29–38 days, depending on the environmental conditions (**Figure 3**). Moreover, about 10–12 generation

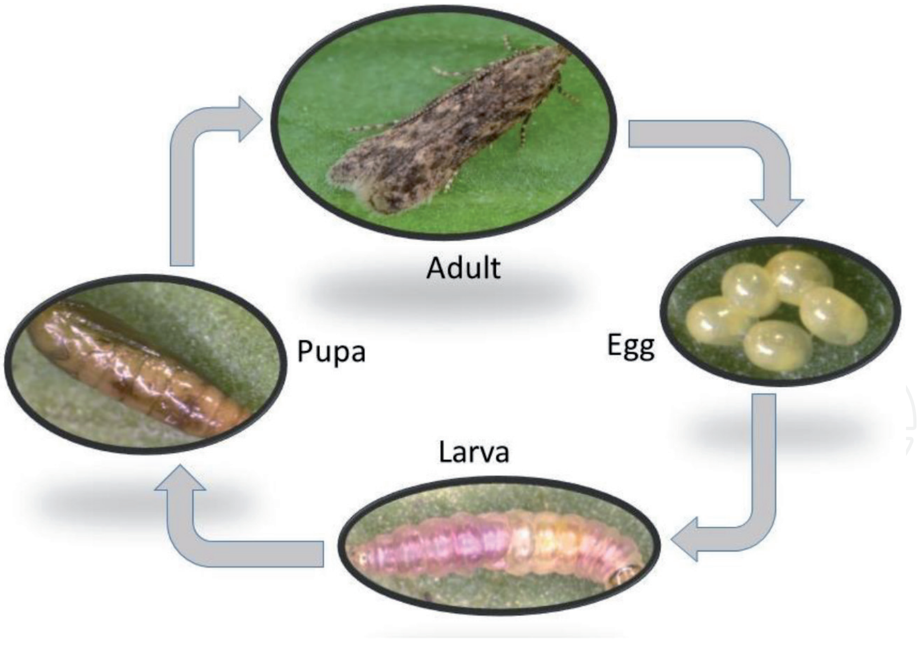

Figure 3.
The life cycle of tomato leafminer, Tuta absoluta (photos: Antonio Biondi; design: Hamadttu A.F. El-Shafie).

may be produced annually. The thermal constant from egg to adult has been estimated to be 453.6 degree days (DD) [19]. TLM larvae do not enter diapause as long as food is available; however, it may overwinter as eggs, pupae, and adults [8, 18].

4. Host range

TLM is an oligophagous feeding on many related species of the family Solanaceae including tomato (*Solanum lycopersicum* L.), potato (*Solanum tuberosum* L.), eggplant (*Solanum melongena* L.), pepper (*Capsicum annuum* L.), sweet pepino (*Solanum muricatum* L.), tobacco (*Nicotiana tabacum* L.), the jimson weed (*Datura stramonium* L.), the African eggplant (*Solanum aethiopicum* L.), and the European black nightshade (*Solanum nigrum* L.) [1, 19, 20]. Sylla et al. [21] reported 12 host plants in the family Solanaceae, 2 in the Amaranthaceae, 2 in the Convolvulaceae, and 1 in the e in native South America, invaded Europe, and Africa. The two hosts in the Amaranthaceae are *Chenopodium album* L. and sugar beet, *Beta vulgaris* L., while the Fabaceae is represented by common bean, *Phaseolus vulgaris*.

TLM prefers tomato on which it is considered as a major pest while it is a minor pest on other alternative hosts. Host plant knowledge is essential for developing integrated pest management (IPM) against *T. absoluta* [21]. Sylla et al. [21] studied the oviposition acceptance, oviposition preference, and performance of two population of TLM from France and Senegal on six solanaceous plants, namely, tomato, eggplant, Ethiopian eggplant, potato, sweet pepper, and pepper. Their findings suggest that there is differentiation in the host range of TLM across invaded areas. In this respect, it has been reported that the relation between the female preference (maternity care) and larval performance should be very tight, as the larvae can survive only on small number of host plants [21].

5. Damage and economic significance

TLM usually attacks the apical buds, flowers, and new fruits of tomato. Larvae make conspicuous mines and galleries on leaves and stems. Damage can occur at any stage of tomato growth from seedlings to mature plant [8]. The larvae feed on the mesophyll tissue, leaving the epidermis intact, thus creating irregular mines and galleries on the leaves (**Figure 4**). The mines and galleries may become necrotic with time. This mining activities lead to reduction of the photosynthetic potential of infested leaves [1]. Infested tomato with TLM show burnt up-like symptoms [9]. The galleries made by the larvae are wider than that caused by the dipteran leaf miner *Liriomyza trifolii* [9, 22]. Larvae can penetrate the axillary buds of young stems when at high density. Thus, it leads to plant withering and check of vegetative growth [8].

After fruit setting, the larvae excavate tunnels in the fruits, which may facilitate invasion by pathogenic agents, resulting in fruit rot (**Figure 5**). The larvae of TLM have a cryptic behavior and endophagous habit, which makes detection of infestation at an early stage difficult [1]. Damage on stems causes necrosis that reduces tomato plant growth and development. Feeding tunnels and holes in the fruits lower their quality and reduce their market value [1]. The serious damage on tomato, due to *T. absoluta*, is caused by the leaf-mining activities and to a lesser extent by tunneling in the fruits [5]. Damage on tomato can reach 100% if no action is taken against the moth. Estimation of economic losses is difficult due to the interaction of many factors including climate, production pattern (greenhouse versus open field), and production costs including seeds, insecticides, fertilization, and other resources. Most of the damage occurs at the early years of invasion, due to lack of farmers' experience on how to manage the pest [1]. Han et al. [23] and Biondi and Desneux [5] summarized the damage of TLM into the following:

1. Production reduction due to injuries on leaves, stems, and fruits

2. Increase in cost of management practices (IPM) against the pest, particularly the purchase and application of insecticides

3. The ban or restriction of fresh tomato, from the side of non-invaded countries, which will affect the economy of countries where TLM is an endemic pest

4. Other costs include the disruption of preexisting integrated pest management (IPM) programs and disturbance of natural ecosystems [24].

Figure 4.
Symptoms of damage appear as mines and galleries on tomato leaves caused by feeding of T. absoluta larvae (photos: Antonio Biondi).

Figure 5.
Tunnels in ripe tomato fruits excavated by the larvae of Tuta absoluta (photos: Antonio Biondi).

6. Invasive potential and global distribution

According to Begon et al. [25], any species distribution is limited and governed by three basic components:

1. The ability of the species to reach a potential site (introduction pathway)

2. Capacity to develop in specific environmental conditions (establishment)

3. The ability to compete with other species occupying the same habitat

TLM is a highly invasive insect pest of tomato crop [1, 6]. The moth was first reported in Europe (Eastern Spain) in 2006 [19]. The introduction in Spain is believed to be from a single population in Chile [26]. Three years later, it was reported in Turkey, the fourth largest producer of tomato in the world, in 2009 [27]. It spread then across Europe and North African countries [6, 28] and Asian countries [23]. According to Seebens et al. [29], most of the invasion occurred during the last 40 years due to increased globalization and trading among continents. The possible introduction pathways for *T. absoluta* include tomato fruits, packing materials of tomato, eggplant and pepper, and planting material [30]. Santana et al. [31] studied the global geographic distribution of TLM using a combination of spatial distribution models as well as the current distribution of the pest. They showed that the suitable areas for *T. absoluta* include North and Central Americas, Africa, Europe, Asia, and Oceania at present time and in the future. Additionally, their model showed that large tomato-producing countries such as China, USA, and Mexico, where the moth is not present, stand a high risk of being invaded by *T. absoluta*. Damme et al. [32] and Han et al. [23] listed important reasons explaining the vast and wide spread of *T. absoluta* around the globe. These reasons include the following:

1. The strong intrinsic invasiveness with high reproductive potential of the moth

2. The dispersal capacity and ability of TLM to adapt to the newly invaded areas. The adults can fly actively for several kilometers, which allows for short distance spread [33].

3. The multivoltine reproductive cycle coupled with high overwintering capacity in greenhouses

4. The strong heat tolerance in open fields

5. Ability of the moth to develop on relatively large number solanaceous and non-solanaceous alternative hosts

The abovementioned reasons are pertaining to the biological traits of the pest. However, there are several reasons connecting human activities and measurements adopted by countries to curb the introduction, establishment, and spread of the pest that also contributed to the vast spread of *T. absoluta* [1, 4, 23, 34]. These reasons are as follows:

1. Weak and ineffective quarantine measures

2. Poor surveillance and phytosanitary measures

3. Bulk trade of untreated fresh tomato products

4. Rapid increase in the size of international trade and transportation of goods

5. Accidental transport of adults and other life cycle stages in consignments through containers and vehicles

6. Lack of joint efforts among affected countries in prevention and containment of the pest

7. Management

Because of its high invasiveness and economic significance, management of *T. absoluta* could be carried out at local, regional, and international levels. The management can be divided into pre-invasion and post-invasion measures. The former are mainly preventive including strict quarantine measures, inspection of tomato consignments, and treatment, when necessary, with proper fumigants before shipping. Endorsement, by countries, of *T. absoluta* as pest of a high risk in quarantine list is essential. *T. absoluta* population management in invaded countries could significantly lower the invasion risk to neighboring non-invaded ones [23, 35]. Establishment of regional network to connect research entomologists, policy-makers, and major stakeholders from all invaded as well as threatened countries [23]. Such network and platforms are supposed to coordinate joint research activities and validation of newly developed management technologies before being applied in the field.

The post-invasion management of *T. absoluta* is to try to eradicate the pest at an early stage of invasion if possible, otherwise a sustainable containment strategy based on integrated pest management is recommended.

In native and invaded areas in the world, current IPM components against TLM include the following:

1. Preventive measures and agronomic control

2. Semiochemically based control using female sex pheromone

3. Biological control

4. Biotechnological control

5. Chemical control by using selective insecticides

7.1 Preventive measures and agronomic control

Preventive and agronomic measures against TLM [36, 37] may include the following:

1. Destruction of previous crop remains to prevent the carryover of the pest

2. Removal of alternative hosts, particularly weeds from the genera *Solanum*, *Datura*, and *Nicotiana*

3. Exclusion of greenhouses with moth-proof sealing

4. Use pest-free planting material (transplants)

5. Screening of existing resistant tomato cultivars

6. Breeding transgenic resistant cultivars

7. Manipulation of soil trait and application of biofertilizers to enhance tomato plant resistance through bottom-up effects

8. Soil cultivation or covering with plastic mulch

7.2 Semiochemically based control

The female sex pheromone can be used in several ways for the management of TLM. These include the following:

1. Monitoring and surveillance. Pheromone-baited sticky traps can be used to monitor all stage of tomato production and across the production chain in nurseries, farms, greenhouses, and packaging and processing facilities [36]. Monitoring of TLM is performed by trapping males and/or by sampling eggs and larvae on infested tomato plants. The latter is however, tedious and difficult to perform over large areas. On the other hand, economic threshold based on male capture is not reliable because trapping process may be affected by

many factors such as population density of the moth, trap designs, and type of pheromone used. Light traps and water traps can also be used to capture both sexes.

2. Male annihilation by mass trapping of adults with pheromone traps (delta traps), which are usually efficient against newly introduced pest when population density is low. For mass trapping, it is recommended to use 20–40 traps/ha. A threshold of 3–4 moths per trap per week need to be reached before the beginning of mass trapping [36].

3. Mating disruption by saturating the atmosphere with sex pheromone, which alters ability of males to locate and find females. This technique can be effectively applied in confined environment such as protected tomato in greenhouses. However, the performance of the technique was poor [17].

7.3 Biological control

Salas Gervassio et al. [38] critically reviewed the natural enemies' complex in tomato agroecosystem. They determined the natural enemies that are suitable for augmentative and conservative strategies in South America and for classical biocontrol agents elsewhere in the world where *T. absoluta* has arrived. The authors reported that more than 50 species and morphospecies of Hymenoptera were associated with *T. absoluta*; however, only about 23 of them could be confirmed as parasitizing the moth. Augmentative biocontrol for *T. absoluta* is commercially available in South America using the parasitoid *Trichogramma pretiosum*, particularly in Brazil, Chile, Colombia, Ecuador, and Peru [38]. The use of endogenous natural enemies for biocontrol of TPW is one of the key points of conservative strategies [39]. The *Macrolophus basicornis* (Stal) and *M. pygmaeus* (Hemiptera: Miridae) are potential biocontrol agents against (egg predators) TLM. The nymphal stage of the former can consume an average of 331 eggs per day, while the adult can feed upon as many as 100 eggs per day [40, 41].

The parasitoids *Necremnus tutae* and *N. cosmopterix* (Hymenoptera: Eulophidae) are potential biocontrol agents against TLM [42].

The predator *Nesidiocoris tenuis* (Hemiptera: Miridae) can be used for the management of other tomato pests including the whiteflies, thrips, leafminers, and aphids [43]. This predator has shown great potential in controlling TPW in Asia [23], Turkey [44], and India [45]. This predator is commercially produced and released against TPW.

Omnivorous mirids had been used against TLM after its arrival in Europe through augmentative and inoculative release in the field and plant nurseries. They are sometimes supplied by conservation strategies using banker plants [1]. The mirid predators *Dicyphus bolivari* Lindberg and *D. errans* (Wolff) Hemiptera: Miridae are potential biocontrol agents against TPW [46].

The generalist egg parasitoid, *Trichogramma achaeae*, is a potential agent for biological control of *T. absoluta*. This worldwide-distributed parasitoid is also attracted by volatiles produced by tomato plants whether uninfested or infested as well as by the sex pheromone of the moth [47]. *Trichogramma evanescens* (Westwood) was also used against TLM in Turkey [44]. The egg parasitoid, *Trichogramma brassicae*, is a potential biocontrol agent of TPW [48]. Hemipteran predators such as anthocorids, geocorids, mirids, nabids, and pentatomids have been identified to be biological agents against *Tuta absoluta* [49]. Since larvae of *Tuta absoluta* are endophagous, cryptically living and feeding inside mines or tunnels in tomato leaves and fruit, respectively, their predation and parasitism by the natural enemies seem to be difficult. Nevertheless, numerous natural enemies can still be used in the management of this notorious pest. The eggs seem to be more vulnerable to predations and parasitism because they are exposed on the surface of tomato growing points. However, the efficacy of natural enemies in suppressing *T. absoluta* populations may be altered by environmental abiotic factors through bottom-up effects triggered by agronomic practices such as irrigation and fertilization. Moreover, plant constitutive and/or induced resistance traits against *T. absoluta* are another source of bottom-up effects, which may interact with irrigation and fertilization and jointly affect the performance and population density of *T. absoluta*, and counterpart natural enemies and their interactions [37]. In addition to the arthropod biocontrol agents, microbial biocontrol agents such as entomopathogenic nematode (EPN) of the genera *Steinernema* and *Heterohabditis* have potential to kill larvae of TLM when they are outside their mines.

7.4 Biotechnological control

Recently, the transcriptome data showed that most of the core genes of RNAi pathway such as Dicer-like and Argonaute and putative orthologous Sid-1 genes are present in *T. absoluta*, suggesting the feasibility of RNAi for controlling this pest [50]. Full plant protection and high larval mortality of *T. absoluta* have not been achieved, probably due to a low expression of dsRNA in transgenic plants [51]. Novel management technologies for TPW include genetically modified crops (GM), for example, GM *Bacillus thuringiensis* (Bt) tomato [52]. RNA interference (RNAi) is a biological mechanism that leads to posttranscriptional gene silencing directed by the presence of double-stranded RNA (dsRNA) molecules [53]. Biotechnically, sterile insect technique (SIT) may also be used for the management of TLM [37]. However, this technique may be compromised if field populations of *T. absoluta* can reproduce by deuterotokous parthenogenesis [17]. It is worth to mention here that these authors reported tychoparthenogensis reproduction of *T. absoluta* under laboratory conditions. They stated that the origin of this type of reproduction could be considered as classical automictic tychoparthenogensis or due to the microbial manipulation by bacterial endosymbiont such as *Wolbachia*, which has recently been identified in *T. absoluta* [54].

7.5 Chemical control

Chemical control of the invasive TLM is difficult; however, its arrival to new invaded areas has been linked to an excessive application of broad-spectrum insecticides [1, 6, 55], in attempts to curb the outbreaks of the pest and to reduce yield losses in tomato crop. Currently, insecticides application seems to be the most commonly used strategy against *T. absoluta* worldwide in open fields of tomato [1, 56–58]. The cryptic behavior and the endophagous habit of larvae make it extremely difficult to control TLM with insecticides [1, 19]. The possible reasons for difficulty of controlling TLM with insecticides, according to Biondi et al. [1] and Guedes et al. [58] include the following:

1. Infestation of tomato by the moth occurs at an early stage of plant growth

2. The multiple attacks by the pest on different plant parts (stems, leaves, buds, young fruit, and ripe fruit)

3. The morphology and architecture of tomato plant that provide protection for feeding larvae against insecticides

Insecticides from different chemical classes were used against TLM in South America, Europe, and other parts of the world. These chemical classes include, but not limited to, organophosphate, pyrethroids, pyrrole, spinosyns, diamides, benzoylureas, and avermactins [54, 56, 59]. Spinosad, azadirachtin, and *Bacillus thuringiensis* toxins (Bt) have been to control TLM in organic tomato production systems [1, 56].

The excessive application of insecticides to prevent and control the outbreaks of *T. absoluta*, particularly in open fields lead to an increased selection pressure which, eventually reduce the effectiveness of such insecticides [58, 60]. For example, when the moth was introduced in Brazil, the farmers initially used insecticides at frequencies of 10–12 applications per cropping season, which was later increased to 30 applications [60]. In Turkey, the annual cost of chemical insecticides used against *T. absoluta* in 2014 was about 160 million Euros [27]. The frequent use of insecticides speeded the appearance of resistance in tomato leaf miner populations, which can migrate outside their geographical range into new invaded areas [1, 6, 56–59].

Guedes et al. [58] reported that enhanced levels of detoxification enzymes and altered target sites are the main resistance mechanisms commonly found in *T. absoluta*. In addition to the development of resistance in TLM populations, due to excessive use of insecticides, compromising of biological control, in tomato agroecosystems, is also not avoidable. In this respect, Soares et al. [43] studied the lethal and sublethal effects of five insecticides (spinetoram, chlorantraniliprole + abamectin, triflumuron, tebufenozide, and abamectin) on adults and the third instar nymph of the predator *Macrolophus basicornis*. They concluded that abamectin caused high mortality in both adult and nymphs. All tested insecticides caused negative effect on the predator.

To overcome the problems of insecticide resistance and other harmful effects on tomato ecosystem, due to the excessive use of insecticides, insecticide resistance management (IRM) strategies are needed to sustain production of tomato crop [1, 58]. Such strategies include adoption of alternative control options such as cultural control, semiochemically based control, biological control, and host plant resistance. All these alternative strategies and tactics would reduce the reliance on insecticides and accordingly the selection pressure on TLM populations [1, 58].

8. Conclusions

Recently, tomato leaf miner has emerged as a highly invasive key pest threatening the global production of tomato. The global commercialization and trade of fresh tomato fruit and transplanting material have accelerated the spread of the pest. The impact of *T. absoluta* on global tomato production industries and on the livelihood of small tomato farming communities in Africa and Asia might be more severe in the coming years, unless great efforts are made to contain its spread. Chemical control of *T. absoluta* with insecticides seems to be ineffective and not sustainable; therefore, alternative management options such as biological control and semiochemically based control should be encouraged. The socioeconomic impact of this moth on subsistent agriculture need to be addressed in future studies.

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