Elucidating *Tuta absoluta* (Meyrick) invasion and enhancing its management in Eastern Africa: spread, socio-ecological impacts, and potential of a newly imported larval parasitoid for classical biological control Eastern in Africa

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ABSTRACT

Agriculture is a fundamental source of sustainable livelihoods in sub-Saharan Africa and millions of people in the region rely solely on small-scale farming for their food security. However, the impacts of invasive alien species (IAS) on crop production are serious, and there is no sign of this abating. Among the recent IAS that have invaded Africa in the last decade, the South American tomato pinworm *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) has been one of the most damaging. Following its first record in the Maghreb region of Africa in 2008, *T. absoluta* rapidly spread throughout Africa with substantial impacts on tomato production, often causing 100% yield loss. Management options adopted against *T. absoluta* by tomato growers in Africa have been based on the use of synthetic insecticides. While chemical insecticide applications arean important component of an integrated pest management programme, misuse and over-reliance often exacerbates the impacts of *T. absoluta* due to the development of resistance to commonly used active substances, increasing the fitness of the pest. This thesis sought to understand the socio-economic impacts of the spread of *T. absoluta* in Eastern Africa and provide effective sustainable pest managementstrategies to reduce its impacts below economic thresholds.

Mapping surveys of *T. absoluta* were conducted in 226 tomato agro-ecosystems across four eastern countries (Kenya, Sudan, Tanzania, and Uganda) Eastern Africafrom 2016 to 2018 to determine the spatiotemporal distribution of the pest. The impacts of *T. absoluta* on the livelihoods of tomato growers were also assessed. Here, 200 tomato growers in Kenya were interviewed using a semi-structured questionnaire. Although *T. absoluta*, a recent invader, was distributed at high infestation levels throughout the subregion (all four countries) and was considered as the the most damaging invasive alien species of agriculturally sustainable livelihoods. The arrival of *T. absoluta* in the subregion has resulted in livelihood losses and increased the cost of tomato production and price of the fruit, and the frequency of pesticide applications. The impact of this pest and the and the absence of effective indigenous natural enemies of the pest in Eastern Africa, was the rationale for the importation of a larval parasitoid, *Dolichogenidea gelechiidivoris* Marsh Syn.: *Apanteles gelechiidivoris* Marsh) (Hymenoptera: Braconidae), of *T. absoluta* from Peru into the quarantine facility of the International Centre of Insect Physiology and Ecology (*icipe*), in Kenya. Pre-release assessments on the parasitzation potential of *D. gelechiidivoris*, encompassing host larval

preference and the host suitability, and its reproductive strategy, for classical biological control of *T. absoluta* in Africa were conducted.

Dolichogenidea gelechiidivoris females preferentially oviposited in early (1st and 2nd) larval instars of *T. absoluta* but parasitized and completed development in all four instars of the host. Host instar did not affect *D. gelechiidivoris* sex-ratio but females reared on the first instar had significantly fewer eggs than when reared in late larval instars (3rd and 4th). Females of the parasitoid emerged with a high mature egg load which peaked 2 d post-eclosion. The females of *D. gelechiidivoris* survived 8.51 ± 0.65 d and produced 103 ± 8 offspring per female at 26 ± 4 °C (range: 24 to 29 °C) and 50–70% relative humidity (RH) in the presence of males and fed honey-water (80% honey). Increasing maternal age decreased the proportion of female offspring. Under the aforementioned laboratory conditions, the Gross and Net reproductive rates were 72 and 39.5 respectively, while the mean generation time was 20 d. The estimated intrinsic rate of natural increase was 0.18. These findings indicate that *D. gelechiidivoris* is a potential biological control agent of *T. absoluta* and should be considered for augmentative/inundative release in Kenya and across Africa following host specificity testing and risk assessments.

The nature of the interaction between *D. gelechidivoris* and the predatory mirid bug *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae), an important and widespread natural enemy of *T. absoluta* in Africa was evaluated because *N. tenuis*, although being a voracious predator of *T. absoluta* eggs, it can also prey on the early host larval instars (1st and 2nd) which are the preferred oviposition host stages of *D. gelechiidivoris*. Here, the impact of *N. tenuis* feeding on *T. absoluta* and the effects on *D. gelechiidivoris* performance was tested. Regardless of the order of introductions (i.e. the sequence of combination with *D. gelechiidivoris*) and densities (i.e. number of *N. tenuis* combined with *D. gelechiidivoris*), there was no intraguild predation by *N. tenuis* on *D. gelechiidivoris* as there was little host larval feeding behaviour. Also, the presence of *N. tenuis* did not affect the oviposition performance of *D. gelechiidivoris*. Further investigations revealed that the combined efficacy of *N. tenuis* and *D. gelechiidivoris* on *T. absoluta* population was significantly higher than either natural enemy alone, thus contributes to the data supporting the release of *D. gelechiidivoris* in Africa. In concluding, integrating *D. gelechiidivoris* and *N. tenuis* in the management of *T. absoluta* could potentially reduce yield losses in tomato in Eastern Africa where the socio-economic impacts of the pest are very serious.

DEDICATION

To my mother

Patricia Omonon Atalor

You have been my oasis in this unchartered journey and throughout my life

Thank you for your love and your loving nature

I love you mama.

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PREFACE

Work from this thesis has been published or submitted for publication in the following international peer-reviewed journals

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DECLARATION

The following thesis has not been submitted to any university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of the author**.**

<u>Pascal Osabhahiemen Aigbedion-Atalor</u>   <u>Date: 19/08/2020</u>

CHAPTER 1

INTRODUCTION

1.1 General Introduction

Under the influence of humans in this epoch, exotic organisms are being transported at an unprecedented rate between regions (Ricciardi et al., 2007) and, in the majority of cases, cause substantial changes to the biodiversity dynamics and ecological services in recipient ecosystems (Asner and Vitousek, 2005; Simberloff et al., 2013). In some cases, global climate change has also been implicated in the migration of species (Furlong and Zalucki, 2017; Mastrandrea et al., 2011; McNeely 2001). These anthropogenically influenced processes have accelerated exponentially, in recent times, following the development of sophisticated mass transportation means, travel, global trade, and general globalization (McNeely, 2001; Pyšek et al., 2012). (). These species may rapidly become invasive – inducing several direct and indirect negative effects in the shape and function of the new environments, consequently changing the innate character of our biological world (Blackburn et al., 2014; Pyšek et al., 2012; Simberloff et al., 2013; Vilá and Ibáñez, 2011). Such species are often referred to, and will be in this thesis, as **I**nvasive **A**lien **S**pecies (hereafter "IAS") (McNeely, 2001).

Presently, there are many IAS threatening ecosystem services, food, and water security as well as the livelihoods of people across the world (see Shackleton et al., 2019 and references therein). Due to its global significance, IAS is ranked as one of the most significant biological threats to the world – as their ecological and socio-economic effects, and consequences thereof, are globally acknowledged (Pyšek and Richardson, 2010; Ragsdale et al., 2011; Suckling and Brockerhoff, 2010). Among the IAS threatening food and livelihood security in Africa, Asia, and Europe is the South American tomato pinworm, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) (the topic of this thesis) (Biondi et al., 2018; Desneux et al., 2010). This pest that originates in the Peruvian central highlands in the western Neotropics, is one of the most recent IAS that constrains the production of tomato, *Solanum lycopersicum* L. (Solanaceae) in the Afro-Eurasian supercontinent (Biondi et al., 2018). Indeed, its impact on tomato production, outside of its native range, since its first detection in eastern Spain in 2006, has been significant (Campos et al., 2017; Desneux et al., 2010; Mansour et al., 2018; Urbaneja et al., 2007). Here, the current distribution, and socio-ecological impacts of *T. absoluta* on local livelihoods in East Africa, as well as pre-release assessments of the potential of a newly-imported larval parasitoid,

Dolichogenidea gelechiidivoris (= *Apanteles gelechiidivoris*) (Marsh) (Hymenoptera: Braconidae), for its control (classical biological control) are investigated.

1.2 *Tuta absoluta*

1.2.1 *Biology*

Tuta absoluta was first described as *Phthorimaea absoluta* by Meyrick in 1917 from a single male collected in the Andes of Peru (Meyrick, 1917). However, following subsequent erroneous descriptions including *Gnorimoschema absoluta* (Clarke), *Scrobipalpula absoluta* (Povolny), and *Scrobipalpuloides absoluta* (Povolny) (Desneux et al., 2010; EPPO, 2005), Povolny, in 1994, correctly placed this species in the genus *Tuta*. The moth is multivoltine, exhibiting a high reproductive potential which promotes the rapid growth of its population (Barrientos et al., 1998; Biondi et al., 2018; Pereyra and Sánchez, 2006). It has a preference for tomato but can attack and complete its development on secondary host plants such as eggplant (*Solanum melongena* L.), potato (*Solanum tuberosum* L.), sweet pepper (*Solanum muricatum* L.), tobacco (*Nicotiana tabacum* L.), and spiny amaranth (*Amaranthus spinosus* L.) (Campos et al., 2017; Desneux et al., 2010; Miranda et al., 1998; Sylla et al., 2019) (see Table 1.1 for further details). Females of this moth preferentially lay eggs on tomato, especially leaves, and the larvae usually hatch at dawn (Desneuex et al., 2010; Tropea Garzia et al., 2012) (Fig. 1.1). The younger instar larvae (i.e. the 1st and 2nd) burrow into the plant (leaves, stems, sepals, and fruits) (Tropea Garzia et al., 2012). Larvae feeding effects on tomato leaves, mainly on leaf mesophyl, produces a thin leaf mine (Biondi et al., 2018). However, following growth, the older instar larvae (3rd and 4th), migrate in search of new feeding niches (Tropea Garzia et al., 2012). Under ideal conditions, good food availability and favourable climatic conditions, larval diapause is rare (Biondi et al., 2018).

The formation of the pupa occurs mainly on host leaves as well as in soil usually surrounded by litter (Desneux et al., 2010). However, pupation can also occur on stems, and fruits (Fernandez and Montagne, 1990; Uchoâ-Fernandes et al., 1995; Viggiani et al., 2009). The pupa of *T. absoluta* is conferred protection by a thin and silky covering (Uchoâ-Fernandes et al., 1995). Pupae become dark brown after five days at 30°C in preparation for adult eclosion (Tropea Garzia et al., 2012). Adults (male and female) usually remain hidden within vegetation during daytime but can exhibit both crepuscular and nocturnal behaviours (Fernandez and Montagne, 1990). Nevertheless, behaviours associated with reproduction, courtship, mating, and oviposition, occur frequently at daytime (Uchoâ-Fernandes et al., 1995). Like other moths,

adults are highly attracted by light sources, especially blue light (Tropea Garzia et al., 2012). Mating period for males is very short (a few hours) compared with 20–22 hours for females (Desneux et al., 2010; Tropea Garzia et al., 2012). Although females can mate about six times in their lifespan, they can mate only once per day, but a mating bout averages about 4.5 hours (Estay, 2000; Lee et al., 2014; Tropea Garzia et al., 2012). The lifespan of females is about 10 and 15 days, while males survive for six to seven days (Estay, 2000). By outliving males, the females become sexually mature when new males emerge (Fernandez and Montagne, 1990). The majority of egg deposition on host plants usually takes place seven days after the first mating, and in this period, a single female can oviposit over 70% of her egg load (Estay, 2000; Tropea Garzia et al., 2012). Females are highly fecund, and a single female can oviposit about 260 eggs in her lifetime (Desneux et al., 2010; Uchoâ-Fernandes et al., 1995). The eggs are deposited either singly or in small batches on young leaves (~73%) stems (~21%), sepals (~5%) and green fruits (~1%) (Estay, 2000).

Table 1.1 Host plant species of *Tuta absoluta* in South America and invasion range (EPPO, 2020)

Host plant species	Family	Host status
Solanum lycopersicum	Solanaceae	Major
Beta vulgaris	Amaranthaceae	Minor
Citrullus lanatus	Cucurbitaceae	Minor
Jatropha curcas	Euphorbiaceae	Minor
Medicago sativa	Fabaceae	Minor
Phaseolus vulgaris	Fabaceae	Minor
Solanum melongena	Solanaceae	Minor
Solanum muricatum	Solanaceae	Minor
Solanum tuberosum	Solanaceae	Minor
Spinacia oleracea	Amaranthaceae	Minor
Amaranthus spinosus	Amaranthaceae	Wild/Weed
Blitum bonus-henricus	Amaranthaceae	Wild/Weed
Datura ferox	Solanaceae	Wild/Weed
Datura stramonium	Solanaceae	Wild/Weed
Lycium chilense	Solanaceae	Wild/Weed
Nicotiana glauca	Solanaceae	Wild/Weed
Oxybasis rubra	Amaranthaceae	Wild/Weed
Solanum dubium	Solanaceae	Wild/Weed
Solanum elaeagnifolium	Solanaceae	Wild/Weed
Solanum habrochaites	Solanaceae	Wild/Weed
Solanum lyratum	Solanaceae	Wild/Weed
Solanum nigrum	Solanaceae	Wild/Weed
Xanthium strumarium	Asteraceae	Wild/Weed

Several studies have documented a correlation between host phenology and *T. absoluta* occurrence. For example, Gomide et al. (2001) and Torres et al. (2001) showed that both host plant phenological stage and the developmental stage of *T. absoluta* determine its distribution within the host's canopy. Gomide et al. (2001) highlighted that numbers of larvae and mines are significantly correlated with expanded leaves in the medium part of the canopy, while a high number of eggs is significantly associated with expanded leaves in the apical part of the plant. These authors showed that *T. absoluta* damage can be estimated by an egg count index. In pre-flowering plants, *T. absoluta* demonstrates an oviposition preference for the undersides of leaves in the apical portion of the plant (Torres et al., 2001). However, at post-flowering, no preference is demonstrated, and both the middle portion and apical part of the plant becomes infested (Torres et al., 2001). The first, second, and third instar larvae are distributed somewhat equally between the apical and the middle parts of the plant in all phenological stages (Tropea Garzia et al., 2012). In contrast, the fourth instar larva is distributed evenly across the plant, including the basal portion (Tropea Garzia et al., 2012). *Tuta absoluta* demonstrates high plasticity to thermal conditions (Krechemer and Foerster, 2015; Martins et al., 2016; Santana et al., 2019). Under optimal conditions, it develops in about 30 days (EPPO, 2005). Barrientos et al. (1998) recorded an average development time of 76.3 days at 14°C, 39.8 days at 19.7°C and 23.8 days at 27.1°C. The latter authors estimated thermal tolerance of *T. absoluta* eggs, larvae and pupae at 6.9 ± 0.5°C, 7.6 ± 0.1°C, and 9.2 ± 1.0°C, respectively.

Volatiles of host plants provide cues for both host-finding and oviposition (Proffit et al., 2011). The availability of secondary host plants (Table 1.1) is a crucial aspect which facilitates the continuous occurrence of *T. absoluta* even when its preferred host, tomato, is absent (Desneux et al., 2010; Mansour et al., 2018). In South America, albeit not inclusive of Argentina where no more than five generations per year occur (EPPO, 2005; Korycinska and Moran, 2009), *T. absoluta* can achieve above 10 generations per year (Tropea Garzia et al., 2012). However, in most of its invasion range, especially in countries with Mediterranean climatic conditions, *T. absoluta* adults can occur throughout the year (Tropea Garzia et al., 2012; Vercher et al., 2010), overwintering either as an egg, pupa, or adult, if food is not available, with a prevalence of pupa in extremely cold periods (Sannino and Espinosa, 2010).

Populations of *T. absoluta* in South America and the invasive range are genetically homogenous (Cifuentes et al., 2011; Shashank et al., 2018). This feature, is, however, not anomalous in species that are recently introduced to novel environments and may be attributed

to founder effects which can greatly reduce genetic variability (Tropea Garzia et al., 2012). In the majority of cases, overtime, introduced populations frequently contain only a subset of the genetic variability of the native populations. However, this is not the case for *T. absoluta* (Shashank et al., 2018; Tropea Garzia et al., 2012). Its gene pool in the invasive populations is similar to that in South America (Shashank et al., 2018; Tropea Garzia et al., 2012). In explaining the cause of this genetic homogeneity, Cifuentes et al. (2011) suggested that the populations occurring in South America are probably invasive. Another possible explanation is the replacement of more susceptible populations, both in South America and in the invasive range, by populations with higher insecticide tolerance (Guedes et al., 2019; Tropea Garzia et al., 2012).
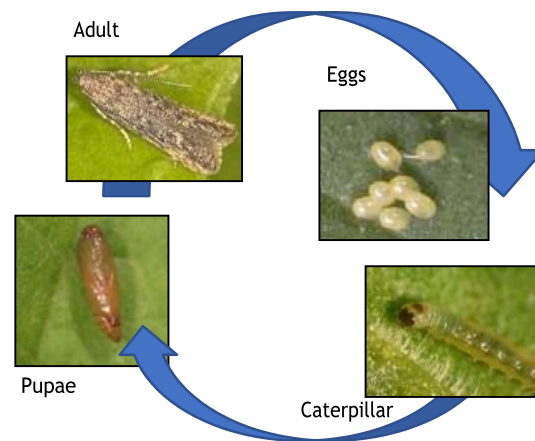
Figure 1.1 Life cycle of *Tuta absoluta*. Photo credit: Kenya Plant Health Inspectorate Service (KEPHIS)

1.2.2 Distribution

1.2.2.1 World distribution

Following the detection of *T. absoluta* in eastern Spain in late 2006 (Urbaneja et al., 2007), the pest has rapidly spread into numerous African, Asian, and European countries (Fig. 1.2) (Biondi et al., 2018; Desneux et al., 2011; Han et al., 2018; Mansour et al., 2018). It has just recently invaded China, the world largest tomato producer (Zhang et al., 2020) and Haiti, Central America (Verheggen et al., 2019). Indeed, the USA, the second largest producer of tomato, is at risk of *T. absoluta* invasion (FAOSTAT, 2016; Han et al., 2018). It is likely that Russia served as the invasion pathway for the spread of the pest into China (Han et al., 2019). The spread of *T. absoluta* in the invasion range has been rapid, averaging 4000 km increase in range every five years (Desneux et al., 2011; Tropea Garzia et al., 2012). Globalization

involving anthropogenic activities has been implicated as the principal pathway facilitating the long-range and rapid spread of this pest (Biondi et al., 2018; Diarra et al., 2014; Tropea Garzia et al., 2012).
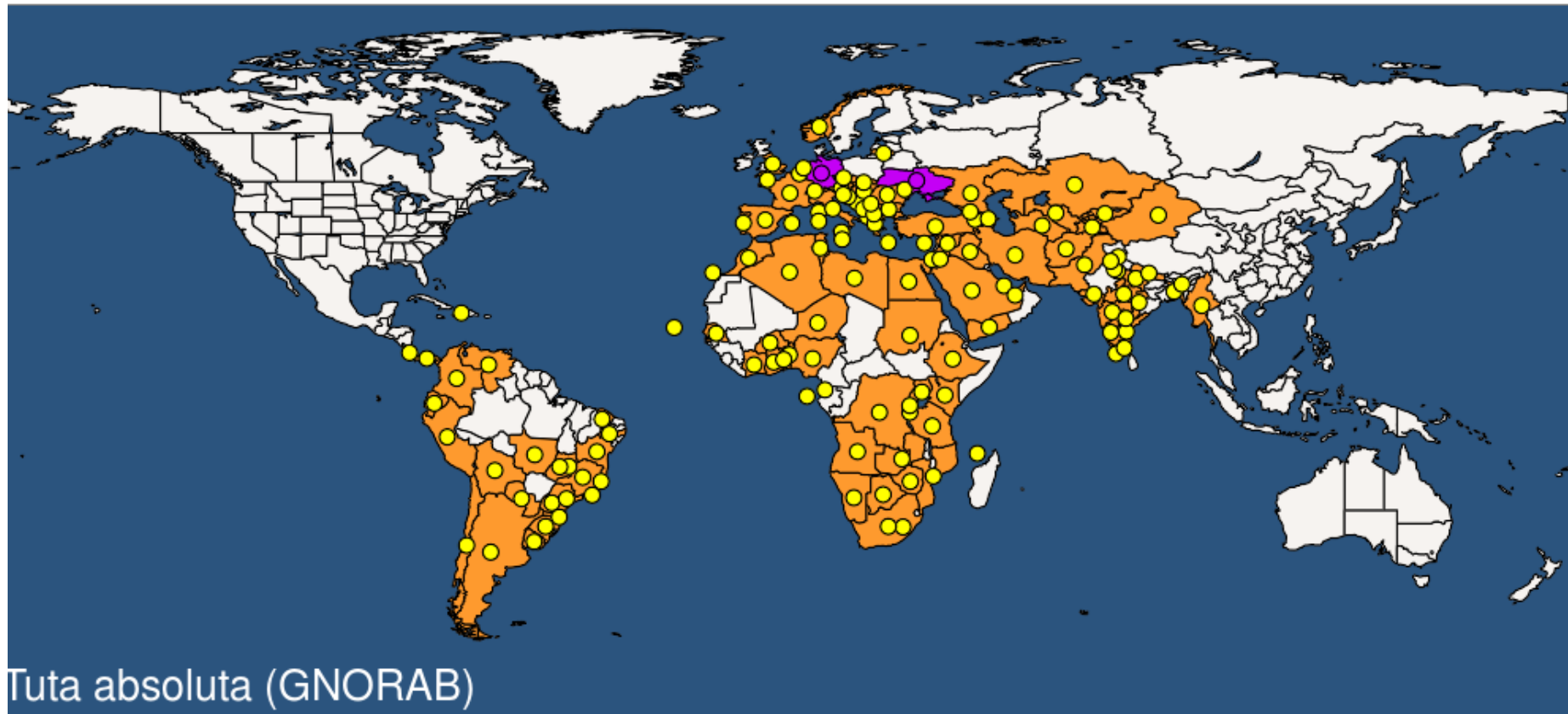
Figure 1.2 The world distribution (as of 2020) of *Tuta absoluta*, and its spread from South America to Europe, Central America, Asia, and Africa (EPPO 2020) https://gd.eppo.int/taxon/GNORAB/distribution but see Santana et al. (2019) https://doi.org/10.1007/s10340-018-1057-y

1.2.2.2 Northern Africa

In Africa, *T. absoluta* was first reported in three countries *viz*: Algeria, Morocco, and Tunisia – in the Maghreb region in 2008 and subsequently in Libya and Egypt in 2009 (EPPO, 2008; 2009; 2011; Guenaoui, 2008; Mansour et al., 2018) (Fig. 1.3). *Tuta absoluta* was first detected in Mostaganem in northwestern Algeria in March 2008 (Guenaoui, 2008), but now occurs in all tomato-producing areas (Mansour et al., 2018). Under greenhouse conditions in the north-eastern part of the country, three generations of *T. absoluta* occur within a short period (Allache et al., 2012). The first male flight occurs in mid-December and densities of all life stages of the pest peak in March (Allache et al., 2012). The pest was first detected in the northern coastal (Mediterranean) region of Nador in Morocco in April 2008 (Ouardi et al., 2012). It has induced serious losses in tomato yield countrywide (Ouardi et al., 2012; Ait Taadaouit et al., 2012; Attrassi, 2015). In Tunisia, *T. absoluta* was first detected at the Governorate of Sousse in October 2008 (Cherif et al. 2013; EPPO, 2009) (Fig. 1.3), and then, it rapidly spread throughout all tomato-producing areas of the country (Mansour et al., 2018, 2019). Between March and July in northeastern Tunisia, *T. absoluta* can develop four to five male flight peaks, albeit higher activities are prevalent subsequently, and three generations of eggs and larvae occur (Cherif and Grissa-Lebdi, 2017; Mansour et al., 2019). However, from November to May, four generations occur (Grissa-Lebdi et al. 2011; Mansour et al., 2019), and flight peaks of *T. absoluta* males are frequently observed between January and May (Cherif et al., 2013). In Egypt, *T. absoluta* was first detected at Marsa Matrouh (northwestern Egypt) in 2009. Since then, it has rapidly spread across the upper and lower regions of Egypt (Moussa et al., 2013; Salama et al., 2015), inducing significant loseses in tomato yield (Moussa et al., 2013). Similar records have also been documented in Libya (Mansour et al., 2018).

1.2.2.3 Eastern Africa

Tuta absoluta spread into sub-Saharan Africa from northern Africa (Mansour et al., 2018), and was first detected in Sudan in 2010 (Mohamed et al., 2012). However, four years later, it spread throughout the rest of Eastern Africa, occurring in South Sudan, Kenya, Ethiopia, Rwanda, Tanzania, and Uganda (Fig. 1.3), with devastating impacts on tomato production (FAO, 2015; Goftishu et al., 2014; Retta and Berhe, 2015). In Kenya, *T. absoluta* was first detected in Mpeketoni and Witu in March 2014, and subsequently in Isiolo and Kirinyaga counties (IPPC, 2014). It has been suggested that it arrived in Kenya through Ethiopia (Mansour et al., 2018). The spread of *T. absoluta* into Tanzania (in 2014), Uganda (in 2015) and other countries in the

region is thought to have been from the established populations in Kenya (Chidege et al., 2016; Tumuhaise et al., 2016; but see Mansour et al., 2018 for recent review).

1.2.2.4 Western Africa

In Western Africa, *T. absoluta* was first detected in Senegal in 2012 (Brévault et al., 2014; Pfeiffer et al., 2013). It was reported in Niger and Cape Verde in 2013 (Adamou et al., 2016), and in Nigeria and Burkina Faso in 2016 (Borisade et al., 2017; Son et al., 2017). It was reported in Ghana in 2017 (IPPC, 2017a), Benin Republic in 2018 (Karlsson et al., 2018), and in Togo in 2019 (Fiaboeet al., 2020). Increasing evidence suggests that it is present throughout the rest of Western Africa (El-Lissy, 2014; FAO, 2018). It has been nicknamed "Tomato Ebola" in Nigeria, the largest tomato producer in Sub-Saharan Africa (FAOSTAT, 2016). In this country, *T. absoluta* was first detected in Daura, Katsina State (northern Nigeria) in April 2015 (Borisade et al., 2017). It was later reported in Kano and Ogun states in late 2015 and has since spread to all the other tomato-producing states with significant loss of tomato-dependent livelihoods (Aigbedion-Atalor et al., 2019).

1.2.2.5 Southern and Central Africa

Except in Madagascar and Mauritius, *T. absoluta* is widespread throughout southern Africa (Mansour et al., 2018) (Fig. 1.3). It is established in the Democratic Republic of the Congo, Equatorial Guinea, and Sao Tome and Principe (Chidege et al., 2017; EPPO, 2018; FAO, 2015; 2018; IPPC, 2017b; 2017c; Luangala et al., 2016; Mutamiswa et al., 2017; Visser et al., 2017). In 2015, Tonnang et al. (2015) predicted the spread of *T. absoluta* into South Africa by 2016. Indeed, it was detected in Mpumalanga Province near the Mozambican border in South Africa in 2016 (IPPC, 2017a). It is currently present in all nine provinces of South Africa (Visser et al., 2017). In Botswana, *T. absoluta* was first recorded in the northeastern district in December 2016 (Mutamiswa et al., 2017), and now occurs countrywide (Mansour et al., 2018). Field surveys of *T. absoluta* conducted in 2016 confirmed the presence of the pest in Muchinga, Copperbelt and Lusaka provinces of Zambia (Luangala et al., 2016). *Tuta absoluta* was first detected in Namibe Province, southwestern Angola in 2017 and has spread countrywide with serious damage ranging between 84% and 100% (Chidege et al., 2017).

Figure 1.3 The occurrence, as of September 2019, and years of first detection of *Tuta absoluta* in each country of Africa. This map, albeit updated, modified, and re-drawn by P. O. Aigbedion-Atalor, was based on the map by Mansour et al. (2018). Numbers – depicting year of first detection – are given as: 08 (2008); 09 (2009); 10 (2010); 12 (2012); 13 (2013); 14 (2014); 15 (2015); 16 (2016); 17 (2017); 19 (2019).

1.2.3 Socio-ecological impacts

All epigeal parts of tomato support the development of *T. absoluta* (Biondi et al., 2018; Desneux et al., 2010; Urbaneja et al., 2013). Larval feeding disrupts the process of photosynthesis (Desneux et al., 2010) (Fig. 1.4). This is the main cause of yield loss (Bogorni et al., 2003). Due to the ability of this pest to attack all developmental stages of tomato, death of tomato seedling occurs following larval feeding (Pereyra and Sánchez, 2006). The numerous wounds on fruits inflicted by the larvae increase the vulnerability of the plant to secondary diseases, notably, bacterial pathogens, which can actively penetrate damaged tissues (Campos et al., 2017). Both in open-fields and greenhouses, larvae can move into fruits through galleries, usually made under the sepals, making the first detection of infested fruits very difficult (Tropea Garzia et al., 2012; Urbaneja et al., 2013) (Fig. 1.4). This is particularly problematic for post-harvest processes (Tropea Garzia et al., 2012; Mansour et al., 2018). In this context, infested fruit for exports can be rejected (Mansour et al., 2018), and now considered as a crucial problem for the tomato industry and its value chain (USDA-APHIS, 2011).

In all the *T. absoluta* infested countries, the cost of tomato production has increased due to the development of management strategies, including early monitoring and phytosanitary measures as well as the use of insecticides (Mansour et al., 2018). For example, in Eastern Africa, in addition to the reduction of marketable quantities, *T. absoluta* has induced significant changes in the cultural perceptions of tomato production (CABI, 2019). Here, due to the frequent application rates of insecticides (every five days) required to curb infestation levels, many tomato growers in the region now consider tomato production monetary daunting and have opted for the cultivation of other crops (CABI, 2019). This has further resulted in the loss of livelihoods in many rural Eastern African communities (see Chapter 2). The impacts of *T. absoluta* in Nigeria has resulted in countrywide destruction of tomato farms and the shutdown of the Dangote tomato processing factory (Borisade et al., 2017). Tomato yield losses due to *T. absoluta* invasion in Nigeria has been estimated at 720000 metric tons (Sanda et al. 2018). In Kano State, for example, over 2 billion Naria (US $ 5,585,822, US $ 1 equivalent to 357 Naria) was reported lost due to the impacts of *T. absoluta* in 2016 (Bala et al. 2019; *Punch Newspaper Online*, 2017). The implications of these significant increases in the cost of production and serious losses in yield were proven t deleterious for producers (Sannino and Espinosa, 2010; USDA-APHIS, 2011).

Figure 1.4 *Tuta absoluta* (A) invades a tomato greenhouse and deposit eggs (B). Developing larvae feed on leaves, stems, and fruits, causing ~ 100% yield loss (C). Larvae continue feeding (D), and develop into pupae, and subsequently to adults (A). Photo credit: Kenya Plant Health Inspectorate Service (KEPHIS). This process also occurs in open-field tomatoes.

1.2.4 Management

Both in the native and invasion range of *T. absoluta*, the use of synthetic insecticides has been the main strategy for its management (Biondi et al., 2018). However, due to their ineffectiveness and detrimental effects on ecosystem functioning, human health, and natural enemies (Le Goff and Giraudo, 2019; Passos et al., 2018), other approaches, such as prophylactic and cultural practices, use of delta traps (pheromone-based trapping systems for early detection, monitoring and/or mass trapping), biological control (the use of predators, parasitoids and pathogens), and botanical insecticides have been adopted in an integrated approach (Caparros Megido et al., 2013; Mansour et al., 2018; Salas Gervassio et al., 2019; Soares et al., 2019).

1.2.4.1 Prophylaxis and cultural practices

It has been highlighted that the integration of holistic and sustainable prophylactic and cultural control measures is crucial to preventing high infestations of *T. absoluta* (Mansour et al., 2018). For example, in Senegal, most farmers seldom grow tomato in the late dry season, due to the high infestation levels of the pest at that time of the year (Sylla et al. 2018). Unfortunately, alternative hosts, such as eggplant and potato can serve as reservoirs for residual populations of the pest (Mansour et al., 2018). Nevertheless, Sylla et al. (2018) have recommended the removal of old eggplant and potato plantations to prevent or reduce the pace of the reconstitution of new populations.

In a few countries, for example in Tunisia and Morocco, the use of insect-proof nets has shown some potential in reducing infestation levels (Cherif et al. 2013; Ouardi et al., 2012). However, this is not the case elsewhere such as Nigeria where Oke et al. (2016) reported that many commercial screenhouses in Nigeria are built with large nets that do not prevent the entrance of *T. absoluta*. Although pyrethroid-treated nets have been reported to have sublethal effects on adults of *T. absouta* (Biondi et al., 2015), this approach is yet to be implemented (Mansour et al., 2018). Recently, a few studies have reported the potential of the use of resistant tomato cultivars against *T. absoluta* (e.g., Cherif et al., 2013; Sohrabi et al., 2016). It has been suggested that tomato cultivars such as cv. Shams and cv. Chebli are not suitable for *T. absoluta* oviposition, implying that infestation levels on these cultivars are usually low (Mansour et al., 2018). Indeed, this has been documented in Tunisia (see, Cherif et al., 2013). Also, in Tunisia, it has been suggested that plastic screens should be used to cover soils to prevent adult

emergence from pupae residing soil litters, and that infested leaves and secondary shoots of the plant removed (Abbes et al., 2012). In Morocco, reports indicate that the destruction of weeds – which serve as secondary hosts for *T. absoluta* – and crop residues, and infested plant materials is crucial for reducing infestation levels of *T. absoluta* (Ouardi et al., 2012).

1.2.4.2 Pheromone-based tools: early detection, monitoring, and mass trapping

The use of traps baited with female sex pheromone lures has now been recognized as an effective tool for monitoring and early detection of *T. absoluta* in novel environments (eg., Machekano et al., 2018). Following detection, traps serve as a useful tool for estimating the pest's density (Mansour et al., 2018), and are crucial for understanding the male flight activity during a growing season (Desneux et al., 2010; Mansour et al., 2018). This strategy provides useful information for implementing control measures (Caparros Megido et al., 2013). For example, in northeastern Tunisia, males of *T. absoluta* in tomato open-field tomatoes are monitored using sex pheromone water traps (Pherodis®), and insecticides are applied when the trap catches reach the recommended threshold (i.e. 50 males per trap per week) (Cherif and Grissa-Lebdi, 2017), thus preventingmisuse of insecticides.

A similar approach, albeit with slight modifications, has been implemented in Algeria, Egypt, and Morocco (e.g., Allache et al., 2012; 2017; El-Aassar et al., 2015; Ouardi et al., 2012; Taha et al., 2013). In Morocco, Ouardi et al. (2012) recommended the use of 20‑25 pheromone traps per hectare in tomato greenhouses and 40‑50 pheromone traps per ha in open-field tomato crops. Taha et al. (2013) highlighted that, in 4200 square meters in Egypt, the average percentage of fruit damage is significantly reduced following mass trapping of males of *T. absoluta* with eight pheromone-baited water traps. In Nigeria, the Nihort-Tuta-Trap tray (water-light traps), in the majority of cases, has been more effective than the application of synthetic insecticides (Oke Abiola: Personal communication).

An alternative to mass trapping is the mating disruption technique (i.e. the confusion of males, disrupting mate location and avoiding/ reducing mating). In Spain and Italy, this residue-free control approach has shown significant successes against *T. absoluta* (Cocco et al., 2013; Vacas et al., 2011). Also, it has been recommended that the effectiveness of the attract (lure)-and-kill technique using the combination "synthetic sex pheromone + insecticide" should be evaluated in Africa (Mansour et al., 2018).

1.2.4.3 Promoting the use of entomopathogens as biorational alternatives

Insecticide formulations that are currently being used for the management of *T. absoluta* include microbial pesticides consisting of bacteria, viruses and fungi and their derivates, plant extracts (botanicals), and synthetic chemicals (Mansour and Biondi, 2020; Mansour et al., 2018). In North Africa, several studies have shown the potential of microbial-based insecticides against *T. absoluta* (Mansour and Biondi, 2020; Mansour et al., 2018). For example, in Tunisia, *Bacillius thuringiensis* var. *kurstaki* has been effective against *T absoluta* (Grissa-Lebdi et al., 2011). Hafsi et al. (2012) showed that seven days after treatment with *B. thuringiensis* var. *kurstaki* (250 g/hl), *T. absoluta* larval mortality ranged between 72 and 80% on the first, second, and third instar larvae of *T. absoluta*.

In Egypt, *B. thuringiensis* (200 g/100 liter) and spinosad (75 ml/100 liter) are effective both for the control of *T. absoluta* larvae and reduction in damage of leaves and fruits (El-Aassar et al., 2015). The evaluation of several plants in Africa has revealed some insecticidal potential for the control of *T. absoluta* (Mansour et al., 2018). For example, the extracts of the plants: *Ricinus communis* L. (Euphorbiaceae); *Argania spinosa* L. (Sapotaceae); *Urtica dioica* L. (Urticaceae); *Thymus vulgaris* L. (Lamiaceae); *Ononis natrix* L. (Fabaceae); *Peganum harmala* L. (Nitrariaceae) and *Lawsonia inermis* L. (Lythraceae) from the Souss valley in Morocco have exhibited some potential against *T. absoluta* larvae (Mansour et al., 2018). The highest mortality rates under laboratory conditions were shown by extracts of *T. vulgaris* leaves (95% mortality) and the seeds of *R. communis* (58% mortality) (Ait Taadaouit et al., 2012, Nilahyane et al. 2012). Also, the essential oil of *Syzygium aromaticum* (L.) buds grown inMorocco, have shown high insecticidal toxicity against the larvae of *T. absoluta* under laboratory conditions (Benchouikh et al., 2016).

Notwithstanding the potential of the microbial-based insecticides in North Africa, synthetic insecticides are still widely used in the region (Mansour and Biondi 2020; Mansour et al. 2018). The insecticide indoxacarb (50 cc/hl) is highly effective for the control of *T. absoluta* larvae (with more than 95% efficacy nine days after treatment), compared to either triflumuron (50 cc/hl) or diafenthiuron (125 cc/hl) (Mansour et al., 2018). Cyromazin (30 g/hl) and flubendiamid (30 g/hl) cause 96% and 77% *T. absoluta* larval mortality respectively (Cherif et al., 2018a). In sub-Saharan Africa, synthetic insecticides are also the main control tool for *T. absoluta* (see Mansour et al., 2018 and references therein). Nevertheless, *B. thuringiensis*,

neem extract, and Spinosad have been registered and available in western Africa (Mansour et al., 2018). Under open-field conditions in central Ethiopia, the application of neem (*Azadirachta indica* (L.)) or *Allium sativum* L. botanical extracts, or the use of the *B. bassiana* have been reported to induce larval mortality of about 70% (Shiberu and Getu, 2018). Despite several advocations against the use of banned insecticides due to their adverse ecotoxicological effects (e.g., Ali et al., 2018), many tomato growers in Africa still use such harmful chemicals such as profenofos for the control of *T. absoluta* (Son et al., 2018).

The first commercially recommended synthetic insecticide, a mixture of chlorantraniliprole and lambda-cyhalothrin (Fanigliulo et al., 2012), has been extensively used in the northern and southwestern parts of Nigeria for the control of *T. absoluta*. However, it has failed to provide significant control (Oke Abiola: Personal communication, 2019). For example, Oke et al. (2017) found that *T. absoluta* was resistant to this insecticide in seven major tomato-producing areas of Nigeria. In Kenya, field surveys conducted in Kirinyaga County (Central Kenya) revealed that 94% of the farmers use synthetic insecticides as the main control option of *T. absoluta*, with chlorantraniliprole (200 g/L) being the most applied active substance (Peris et al., 2018). A recent study (Chapter 2) showed that all tomato growers in four counties (Machakos, Kajiado, Kwale, and Taita Taveta) of Kenya rely on synthetic insecticides for the control of *T. absoluta*.

Although the application of synthetic insecticides is the main control of *T. absoluta* on tomato worldwide (Biondi et al., 2018; Campos et al., 2017), it is, however, seldom effective and sustainable, and can cause dramatic increases in the frequency of required applications, due to the pest's resistance, and pest control related costs (Mansour et al., 2018). Indeed, following the arrival of *T. absoluta* in Europe and Africa, insecticide resistance has been a serious problem in the development of control systems (Biondi et al., 2018; Guedes et al., 2019; Mansour et al., 2018). Such a situation is the result of the selection pressure both in South America and in its invasion range (Mansour et al., 2018). The early cases of resistance were reported from South America because of the reliance and overuse of organophosphate and pyrethroid insecticides (Lietti et al., 2005; Siqueira et al., 2000; Salazar and Araya, 1997). Also, negligible to moderate levels of resistance to indoxacarb and extreme resistance to chitin synthesis inhibitors and spinosad have been documented (Campos et al., 2014; Guedes et al., 2019; Reyes et al., 2012; Silva et al., 2016).

Tuta absoluta has demonstrated a serious potential of rapidly developing resistance to multiple classes of insecticide and this calls for concern. In elucidating this, Mansour et al. (2018), in a recent review, emphasized that although only little data on insecticide resistance are currently available in Africa, it is, however, likely that the serious proliferation and destructive potential of *T. absoluta* will result in further resistance due to the significantly increasing insecticide application frequency. In addition to resistance, other major pitfalls associated with the application of synthetic insecticides include detrimental side effects on non-target beneficial arthropods (Arnò and Gabarra, 2011; Biondi et al., 2012; 2013a; 2013b; Cherif et al., 2018b; Mansour and Biondi, 2020; Wanumen et al., 2016 but see Desneux et al., 2007).

1.2.4.4 Biological control

In addition to the use of pathogens (described in section *1.2.4.3*) several predatory and parasitoid species have been identified globally (Ferracini et al. 2019; Salas Gervassio et al., 2019), and are currently being used for the control of *T. absoluta* in Africa and beyond. The predators are chiefly hemipterans and belong mainly to three families *viz.* Miridae, Anthocoridae and Nabidae (Ferracini et al. 2019; Mansour and Biondi, 2020; Zappalá et al., 2013). In North Africa, these predatory bugs have been studied extensively and are currently considered "promising" for the suppression of *T. absoluta* albeit in combination with other control agents and methods such as pheromone traps, parasitoids, and botanical insecticides (Ferracini et al. 2019; Mansour and Biondi, 2020; Zappalá et al., 2013).

Among the predatory bugs, the cosmopolitan predators *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae) and *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae) are the most voracious, occurring spontaneously almost all year round both in screenhouses and open-field tomato crops (Ferracini et al. 2019; Mansour and Biondi, 2020; Zappalá et al., 2013). Several of the known parasitoids of *T. absoluta* in Africa are species of the families Braconidae, Eulophidae and Trichogrammatidae (Table 1.2). The integration of these natural enemies for the control of *T. absoluta* has been recommended to mitigate the overreliance on synthetic insecticides (Mansour and Biondi, 2020; Mansour et al., 2018).

Table 1.2 Natural enemies (predators and parasitoids) of *Tuta absoluta* and their distribution in Africa

Natural enemy	Family	Species	Host stage(s) attacked	Distribution	Reference(s)
Predators	Anthocoridae	*Orius sp.*	Eggs, larvae, and pupae	NA	Salehi et al. (2016)
		Orius albidipennis	Eggs and larvae	N/SSA	Al-Jboory et al. (2012)
	Miridae	*Dicyphus errans*	Eggs and larvae	NA/WA	Ingegno et al. (2019), Oke Abiola: Personal communication, 2019)
		Dicyphus tamaninii	Eggs and larvae	NA	Guenaoui et al. (2011a)
		Macrolophus caliginosus	Eggs and larvae	NA	Guenaoui et al. (2011a)
		Macrolophus pygmaeus	Eggs and larvae	N/SSA	Mansour et al. (2018)
		Nesidiocoris tenuis	Eggs and larvae	N/SSA	Mansour et al. (2018)
	Lycosidae	*Tanimlanmamis sp.*	Larvae and pupae	NA	Öztemiz (2012)
	Phytoseiidae	*Amblyseius swirskii*		NA	Elaini (2011), Ouardi et al. (2012)
	Reduvidae	*Rhynocoris segmentarius*	Eggs and larvae	SA	Mansour et al. (2018)
Parasitoids	Chalcidae	*Hockeria* sp	Pupae	SA	Mansour et al. (2018)
	Ichneumonidae	*Hyposoter didymator*	Larvae	NA	Boualem et al. (2012)
	Braconidae	*Apanteles sp*	Larvae	WA	Oke et al. (2016)
		Bracon sp.	Larvae	NA	Tropea Garzia et al. (2011)
		Bracon didemie	Larvae	NA	Doğanlar and Yiğit (2011)
		Bracon hebetor	Larvae	EA/NA	Ferracini et al. (2012)
		Bracon nigricans	Larvae	NA	Gabarra et al. (2014)
		Dolichogenidea appellator	Larvae	EA	Idriss et al. (2018)
	Eulophidae	*Diglyphus sp*	Larvae	NA	Zappalà et al. (2013)
		Diglyphus isaea	Larvae	NA	Gabarra et al. (2014)
		Elasmus sp.	Larvae and pupae	NA	Eman et al. (2016)
		Hemiptarsenus ornatus	Larvae	NA	Zappalà et al. (2013)
		Hemiptarsenus zilahisebessi	Larvae	NA	Guenaoui et al. (2011a; 2011b)
		Necremnus tutae	Larvae	NA	Gebiola et al. (2015)
		Neochrysocharis formosa	Eggs and arvae	EA/NA	Boualem et al. (2012).
		Neochrysocharis sp.	Larvae	NA	Boualem et al. (2012).
		Stenomesius sp	Larvae	NA	Boualem et al. (2012).
		Sympiesis sp	Larvae	NA	Boualem et al. (2012).
	Platygastridae	*Telenomus* sp	Eggs	NA	Eman et al. (2016)

Table 1 continued

Trichogrammatidae	*Trichogramma achaeae*	Eggs	NA	Kortam et al. (2014)
	Trichogramma bourarachae	Eggs	NA	Zouba et al. (2013b)
	Trichogramma cacoeciae	Eggs	NA	Cherif et al. (2019), Mansour et al. (2019)
	Trichogramma euproctidis	Eggs	NA	Zappalà et al. (2013), El-Arnaouty et al. (2014)
	Trichogramma evanescens	Eggs	NA	Goda et al. (2015), Rizk (2016)

Abbreviations with the distribution column indicate the following EA = Eastern Africa, WA = Western Africa, NA = Northern Africa, SA = Southern Africa, SSA = Sub-Saharan Africa, N/SSA = Northern and Sub-Saharan Africa, EA/NA = Eastern and Northern Africa, NA/WA = Northern and Western Africa.

1.3 *Dolichogenidea gelechiidivoris* **(Marsh)** **(***=Apanteles gelechiidivoris***) (Marsh) (Hymenoptera: Braconidae)***: **a potential classical biocontrol agent of** *Tuta absoluta* **in Africa**

1.3.1 Description

The following description was derived from Marsh (1975).

- **Female**: Body length of female *Dolichogenidea gelechiidivoris* (Marsh) (*=Apanteles gelechiidivoris*) (Marsh) (Hymenoptera: Braconidae) is 2.5 mm. Its body is black, except the mandibles, palpi, apices of femora, tibiae and tarsi which are black brown. The pterostigma is translucent and margined by brown wing veins. The malar space in the head is about as long as clypeus. The antennae are shorter than the body. The thorax is stout with a smooth and shining propodeum on the dorsal surface which is slightly rugose laterally and strongly rugose medially at the apex. The wings are short and broad, with a vannal lobe evenly convex with fringes of hair. The abdomen is short. The first tergum is slightly narrower at the apex than at the base, longer than apical width, smooth at the base, and rugose at the apex. The second tergum is nearly four times wider than the apical width and two times the size of the basal width. The ovipositor is like the hind tibia in length but curved downward.

- **Male**: Similar to female, except that the antennae are longer than the body, and the median plate of first the tergum is slightly narrower than that of females at the apex, while the median plate of second the tergum is slightly longer.

- **Eggs**: The eggs are elongated and smooth; the front is round, and the back has a hook typical Hymenoptera eggs with a size of about 0.60 x 0.08 mm. Newly oviposited eggs are translucent and then a dark portion in the central part occurs after a few hours.

- **Larva**: *Dolichogenidea gelechiidivoris* has three larval stages, the first is the mandibulate-caudate type (approximately 0.46 x 0.12 mm); the second (1.49 x 0.29 mm); and third (4.92 x 0.59 mm) stages are hymenopteriform. At the end of the third larval instar, the larvae kill and leave the host, and later builds a white cocoon.

- **Pupa:** The pupa is the exarate type (with the appendages free and not glued to the body) and about 4.92 x 1.7 mm in size. It develops inside the cocoon made by the mature last instar larva soon after it emerges from the host.

1.3.2 Origin and distribution

There is a lack of literature on *D. gelechiidivoris*. However, it is a Neotropical species adapted to wide ecological amplitude occurring in the coastal regions and Andean highland of Peru, Colombia, and Chile (Mujica personal communication 2018). It has been recovered at altitudes from 2800 (Hausahuasi) to 3850 (Mantaro Valley) m asl in central Peruvian highlands (Kroschel and Canedo, 2009). It has also been recorded in the central Peruvian lowlands such as the Canete Valley (Mujica personal communication 2018), representing 14% of the total parasitoid guild collected from untreated potato fields (Mujica and Kroschel, 2013). *Dolichogenidea gelechiidivoris* is an important parasitoid of *T. absoluta* and *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) in La Molina, Rimac Valley in Peru (Redolfi and Vargas 1983). Fernandez and Montagne (1990) documented that *D. gelechiidivoris* was recovered from *P. operculella* infested tomato fields in Venezuela. Also, Marsh (1975) mentioned that *D. gelechiidivoris* was released in California against *P. operculella*, and *Keiferia lycopersicella* (Walsingham) (Lepidoptera: Gelechiidae). This wasp was also released in Hawaii for the control of *K. lycopersicella* (Nakao and Funasaki, 1979).

1.3.3 Host species

Dolichogenidea gelechiidivoris is a solitary oligophagous larval endoparasitoid of *T. absoluta* and a few other closely related gelechiidae species (Mujica and Kroschel, 2013; Palacious and Cisneros, 1995) (Table 1.3). There is no record of *D. gelechiidivoris* parasitizing any host species that are not in the Gelechiidae family, strongly suggesting that it has a narrow host range; which is an important attribute for any candidate exotic natural enemy under consideration for a classical biological control programme.

Table 1.3 Hosts of *Dolichogenidea gelechiidivoris*

Gelechiidae host	Countries	References
Tuta absoluta (Meyrick)	Chile, Colombia, Peru	Palacious and Cisneros, (1995); Bajonero et al. (2008)
Phthorimaea operculella (Zeller)	Peru, Venezuela	Palacious and Cisneros (1995); Mujica and Kroschel (2013)
Keiferia lycopersicella (Walsingham)	USA (Florida & Hawaii)	Nakao and Funasaki (1979)
Symmetrischema tangolias (Gyen)	Peru	Redolfi and Vargas 1983

CIP indicates the International Potato Centre, Peru

1.3.4 Parasitism

This parasitoid exhibits arrhenotokous parthenogenesis and high parasitic capacity (Bajonero et al., 2008). Under suitable temperature conditions, ranging between 20 and 26°C (Bajonero et al., 2008), two *D. gelechiidivoris* females on a host plant infested by *T. absoluta* can negate economic damage thresholds (Cely et al., 2006). In South America, the effectiveness of *D. gelechiidivoris* has received much attention since the late 1900s (e.g., Agudelo and Kaimowitz, 1997; Bajonero et al., 2008; Desneux et al., 2010; Palacios and Cisneros, 1995; Valencia and Penaloza, 1990; Vallejo, 1999; Wanumen, 2012). Periodic field surveys conducted in the central Coast of Peru in the late 1980s and early 1990s showed that *D. gelechiidivoris* was the most prevalent parasitoid of *T. absoluta*, achieving about 26 – 41% and 57% parasitism with and without the use of chemical pesticides, respectively (Palacios and Cisneros, 1995). Parasitism rates of ≈59% (Agudelo and Kaimowitz, 1997), 70% (Valencia and Penaloza, 1990), and 77% (Vallejo, 1999) have been reported in Colombia. In Chile, *D. gelechiidivoris* was initially thought not to be established following its introduction from Colombia in the mid-1980s (Rojas, 1997). However, 10 years later, high parasitism levels were recorded, and it is now considered as one of the most important parasitoids of *T. absoluta* in the country (Desneux et al., 2010).

1.4 Rationale for the study

Since the first detection of *T. absoluta* in the Maghreb region of Africa in 2008 (Mansour et al., 2018), it has spread (as at September 2019) into 46 of the 54 countries in Africa (Fig. 1.3), and the other eight countries are potentially threatened (Guimapi et al., 2016; Tonnang et al., 2015) (Fig. 1.5, Fig. 1.6, and Fig. 1.7). Three distinct phases occur in the course of virtually every biological invasion: (1) arrival (the process by which organisms are transported outside their native range); (2) establishment (the process by which the introduced population grows to the extent where eradication becomes unfeasible); and (3) spread (the further expansion of the population in the new range) (Blackburn et al., 2014). In its invasive range in Africa, all three invasion phases of *T. absoluta* have been completed with serious impacts on tomato production (e.g., FAO, 2015; Mansour et al., 2018) and indigenous livelihoods (CABI, 2019). Biological control of invasive insect pests in Africa is a promising control alternative to the use of broad-spectrum insecticides as shown, for example, by the successful control of the Cassava mealybug *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae) (Neuenschwander, 2001). In North Africa, a few indigenous *Trichogramma* egg parasitoids have been mass-released to help manage *T. absoluta* in the region and beyond (e.g., Cherif et

al., 2019a; El-Arnaouty et al., 2014; Kortam et al., 2014; Mansour and Biondi, 2020; Rizk, 2016; Zouba et al., 2013a). Although these parasitoids are not capable ofsuppressing the population density of *T. absoluta* below economic thresholds, they are, however, promising (Mansour and Biondi, 2020; Mansour et al., 2018). Therefore, to complement the efforts of these effective indigenous parasitoids in Africa, the International Centre of Insect Physiology and Ecology (hereafter "*icipe*") in Kenya, in collaboration with the International Potato Centre (hereafter "CIP") in Peru identified an effective endemic natural enemy in the native range (Peruvian central highlands) of the pest as a potentially suitable candidate. Subsequently, *D. gelechiidivoris* was identified and imported into Kenya from Peru in 2017 for classical biological control of *T. absoluta* in Kenya and beyond.
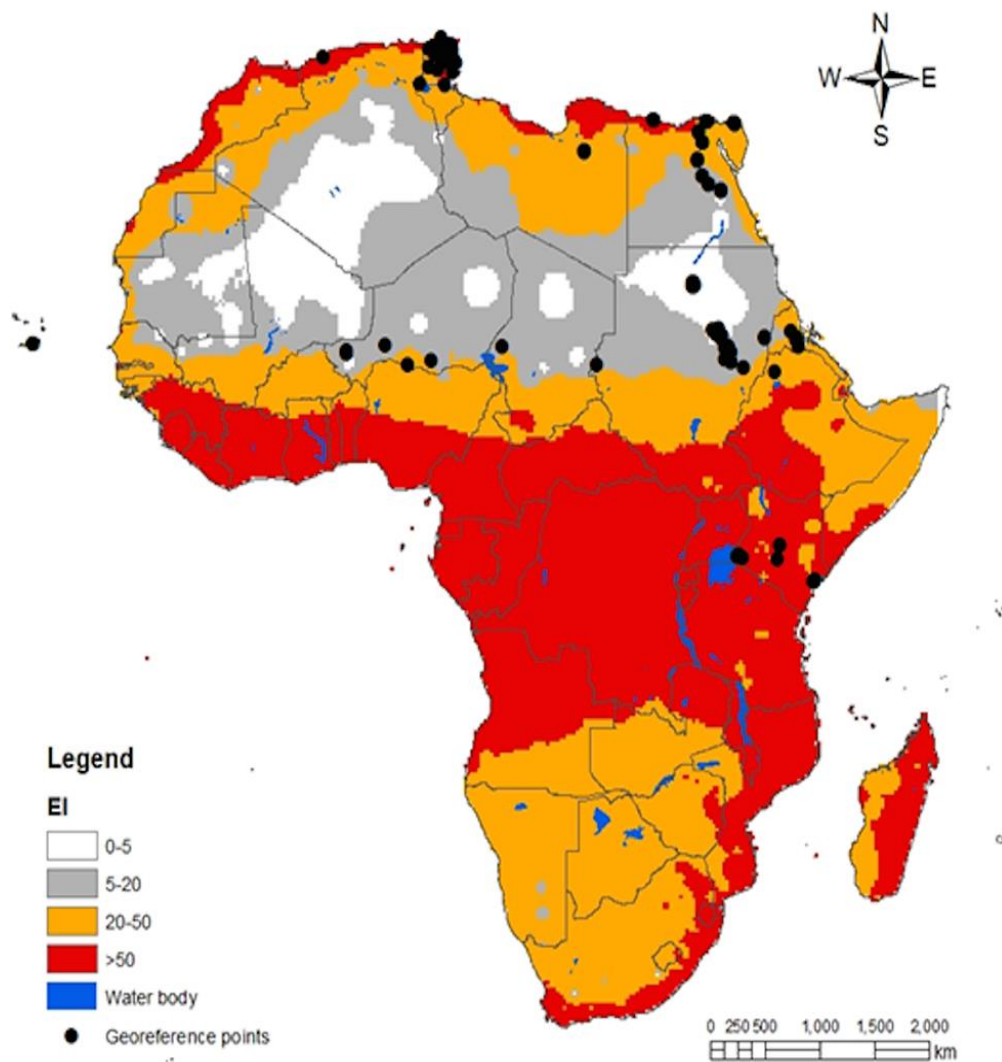
Figure 1.5 CLIMEX climatic suitability indices for *Tuta absoluta* in Africa. Predictions are based on the eco-climatic index (*EI*), a measure of climatic suitability scaled from 1–100, for locations within CLIMEX's station database. *EI* = (0–5) location is not suitable; *EI* = (5–20) moderate level of suitability; *EI* = (20–50) high risk of establishment and *EI* > 50 very high likelihood of long-term survival. The black dotes are the geo-reference location points obtained from surveys (Tonnang et al., 2015).
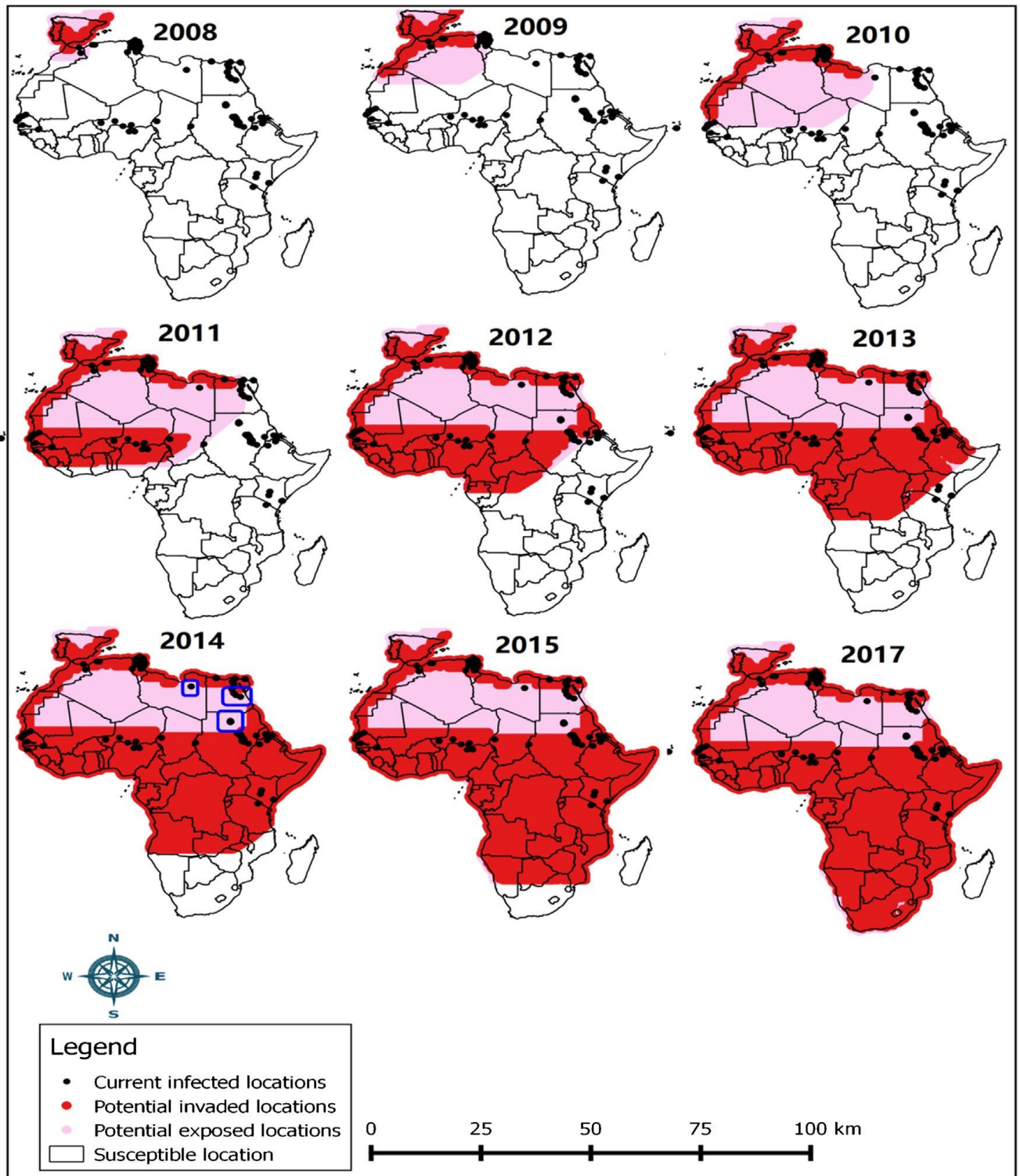
Figure 1.6 The spread of *Tuta absoluta* in Africa obtained through a 10-year simulation taking into account humidity and temperature as parameters for the pest propagation. The geo-referenced points in black represent locations of occurrence of *Tuta absoluta* and the areas in white are susceptible locations. Zones in pink are zone at low risk of invasion and spread of the pest. Zones in red represent zones at high risk of invasion and spread of the pest. The simulations were carried out within the 10-year period from 2008 to 2017. Areas in blue colour in the year 2014, represents zones of mismatch requesting an improvement of the model Guimapi et al. (2016).

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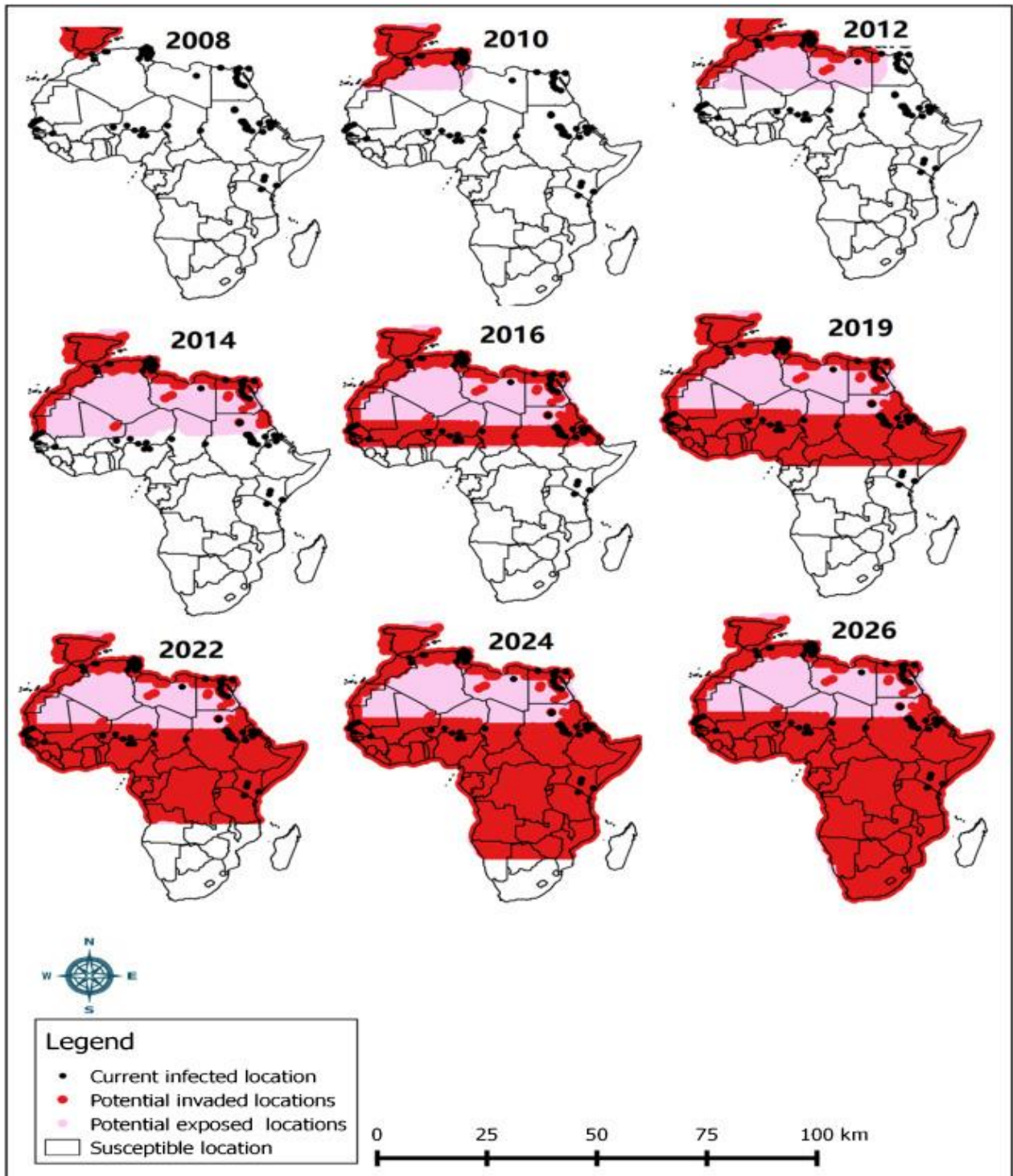
Figure 1.7 The spread of *Tuta absoluta* in Africa obtained through a 10-year simulation taking into account vegetation, humidity, temperature and yield of tomatoes production as parameters for the pest propagation. The geo-referenced points in black represent locations of occurrence of *Tuta absoluta* and the areas in white are susceptible locations. Zones in pink are zone at low risk of invasion and spread of the pest. Zones in red represent zones at high risk of invasion and spread of the pest. The simulations are carried out within the 10-year period from 2008 to 2017. Areas in blue colour in the year 2014, represents zones of mismatch requesting an improvement of the model Guimapi et al. (2016).

1.5 Problem statement

Widely considered as a vegetable, tomato is one of the most economically important fruit crops throughout the world (CABI, 2019; Desneux et al., 2010). Its annual global production is about 182 million tonnes, equating to about US$ 87.9 billion (CABI, 2019). In Africa, tomato is the most consumed fruit, both in its raw and processed forms (CABI, 2019). In Kenya, it is one of the major vegetable crops produced and it accounts for about 14% of the total vegetable production in the country (GoK, 2012; Wafula et al., 2018). It is considered as the most lucrative vegetable crop in terms of enterprise value per acre (GoK, 2012), and a fundamental socio-economic driver of sustainable livelihoods, notably, among rural dwellers who are reliant on agriculture for their livelihoods (CABI, 2019; Sigei et al., 2014; Wafula et al., 2018). Significantly, it provides livelihood means for women who constitute over 60% of the labour force along the tomato value chain in Africa (CABI 2019). Furthermore, tomato confers an affordable rich nutritional value (vitamins, minerals, and essential amino acids) to anthropogenic health, especially in impoverished rural communities (CABI 2019). Alas, like many other important horticultural crops, its production is constrained by several biotic and abiotic factors, and amongst the biotic factors, *T. absoluta* is the worst in Eastern Africa and beyond (Biondi et al., 2018; CABI, 2019; Diarra et al., 2014). As previously mentioned (section 1.2.4), chemical control, albeit the main control strategy against *T. absoluta* in Africa, is not sustainable and currently less effective due to over-reliance and misuse (Guedes and Picanço, 2012; Guedes et al., 2019; Mansour et al., 2018). This is further complicated by the feeding behavior of the pest (Desneux et al., 2010). In this context, the destructive four instar larvae of the pest are conferred protection by leaf tissues within the mines formed (Desneux et al., 2010; Mohamed et al., 2015). When in high abundance, excessive leaf mining by the larval feeding and tunneling within mesophyll cells of the leaves disrupts the free movement of CO_2, and consequently, the overall photosynthetic process of the plant (Desneux et al., 2010), thus inducing serious yield losses (Biondi et al., 2018; Desneux et al., 2010).

1.6 Hypotheses compendium

(i)   *Tuta absoluta* is widespread in Eastern Africa and a significant stressor of tomato-dependent livelihoods

(ii)   *Dolichogenidea gelechiidivoris* will accept *T. absoluta* larvae for oviposition and the host instar larvae will support the juvenile development of the parasitoid

(iii)   The predation on *T. absoluta* larvae by *N. tenuis* will inflict intraguild predation on *D. gelechiidivoris* and reduce the performance of the parasitoid.

1.7 Objective

To determine the spread and socio-ecological impacts of *T. absoluta* in Eastern Africa and evaluate the potential of a newly imported larval parasitoid, *D. gelechiidivoris* for classical biological control of *T. absoluta* in Eastern Africa.

1.7.1 Specific objectives

Specifically, this thesis intends to:

(i)   Determine the spread and socio-ecological impacts of *T. absoluta* in Eastern Africa.

(ii)   Assess the host stage preference, acceptability, and suitability of *D. gelechiidivoris*.

(iii)   Evaluate the direct and indirect interactions between *D. gelechiidivoris* and *N. tenuis.*

CHAPTER 2

The distribution and socio-economic impacts of *Tuta absoluta* (Lepidoptera: Gelechiidae) in Eastern Africa*

2.1 Introduction

In novel ranges, there is overwhelming evidence showing that IAS can cause increase in the vulnerability of livelihoods (Shackleton et al., 2019 and references therein). This is mainly attributed to their ability of altering (directly or indirectly) livelihood assets and strategies as well as transformative structures and processes (Shackleton et al., 2019). In the majority of cases, these transformations consistently impact livelihood outcomes and overall human well-being in a negative manner (Shackleton et al., 2019). Although the importance of these socio-ecological dynamics of IAS have long been recognized, studies on biological invasions, however, are frequently skewed towards understanding the ecological aspects such as effects on crop production, biodiversity, and the consequences thereof, with no or negligible efforts directed towards the understanding of the social dimensions, such as impacts on human livelihoods and well-being (Blackburn et al., 2014; McNeely, 2001; Shackleton et al., 2019). For example, the impacts of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) on tomato production in its invaded range is clearly articulated (Biondi et al., 2018; Desneux et al., 2010; Mansour et al., 2018), but its impacts on livelihoods remain unclear and no studies of its socio-economic impacts in Africa have been conducted. However, historical records on the impacts of invasive pests in Africa clearly show the significance of socio-economic dimensions relating to livelihood losses and household impacts. A classic example is the invasion by the oriental fruit fly *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae). It has been documented that since the first detection of *B. dorsalis* in Kenya in 2003 (Lux et al., 2003), this pest has spread throughout Africa with serious impacts on millions of households (Badii et al., 2015).

Although *T. absoluta* is widespread in Eastern Africa, its distribution and impacts on tomato growers across the sub-region are unclear. Furthermore, indigenous perception of IAS, including *T. absoluta*, is considered under-represented in the scholarly discourse (Bhattacharyya and Larson, 2014). This chapter addresses this lacuna in Eastern Africa using Kenya as a case study. Here, indigenous voices from Kenya were used to assess the local

awareness and impacts of *T. absoluta* on tomato-dependent livelihoods in Kenya in relation to the five domains of sustainable livelihood framework described by Chambers and Conway (1992) and Scoones (1998) on tomato growers in the sub-region. In addition, the distribution of *T. absoluta* across four countries in the sub-region was mapped and the infestation levels of *T. absoluta* in Kenya were assessed.

2.2 Materials and methods

2.2.1 Study sites

Mapping surveys of *T. absoluta* were conducted in four Eastern Africa countries: Kenya, Sudan, Tanzania, and Uganda. Livelihood impact surveys were conducted in four counties – Kajiado, Kwale, Machakos, and Taita Taveta – of Kenya (Fig. 2.1), which are considered major tomato-producing counties in the country (Sigei et al., 2014). In Kajiado (1° 50' 30.984" S 36° 47' 21.3648" E), the average annual temperature and rainfall are 19°C and 500 mm respectively. In Kwale (4° 10' 31.116" S 39° 27' 11.952" E), the climate is monsoonal, being hot and dry between January and April, and between June. The average annual temperature and rainfall are about 24°C and 1040 mm respectively (MoALF, 2017). In Machakos (1° 31' 6.348" S 37° 16' 0.8364" E), temperature varies between 18°C to 29°C, with the coldest month being July and the warmest period occurring between October and March. Average annual rainfall is about 800 mm. Taita Taveta county (3° 23' 31.92" S 37° 40' 26.8392" E) which is divided into eight agro-ecological zones receives an annual average temperature and rainfall of about 23°C and 650 mm respectively (MoLAF, 2017). Tomato is grown in these counties mainly by small-scale farmers.
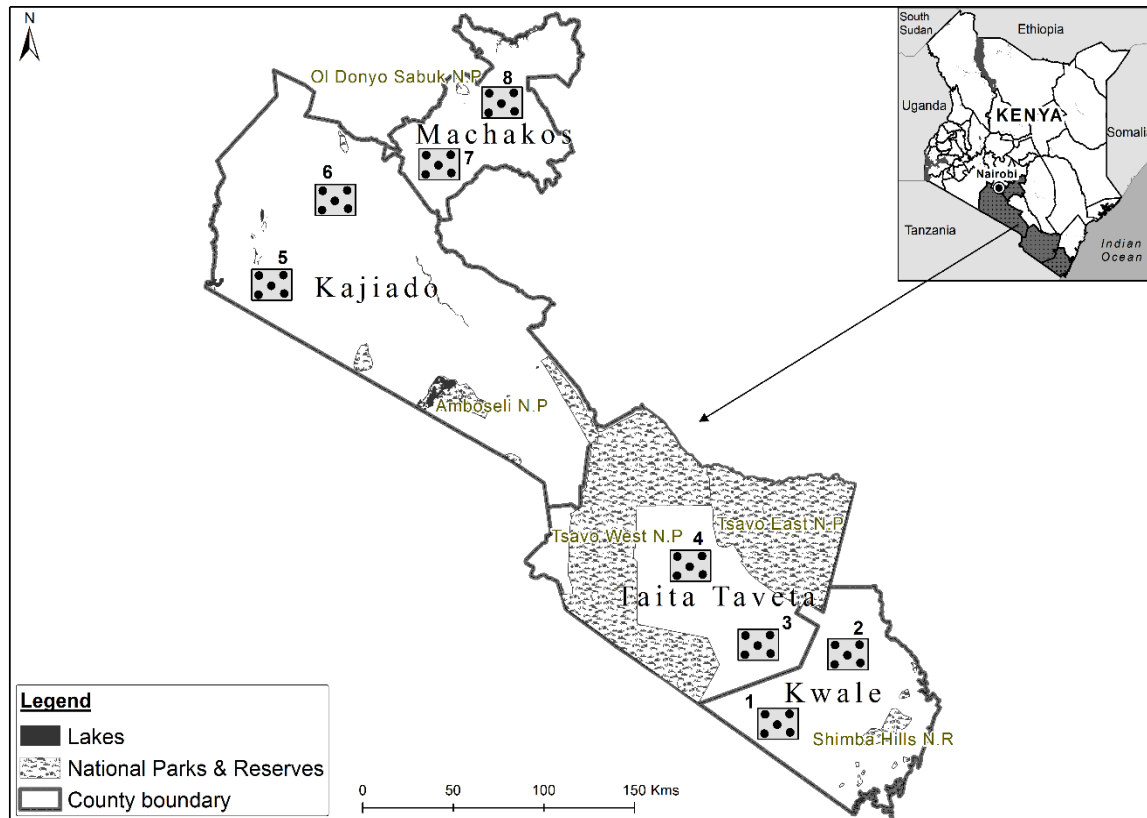
Figure 2.1 The four counties of Kenya where the infestation levels and impact (livelihood surveys) of *Tuta absoluta* were estimated. Numbers and grey shaded boxes indicate locations sampled. 1 Shimba Hills, 2 Mabokoni-Kinondo, 3 Challa, 4 Njukini, 5 Engutoto, 6 Elangata, 7 Mbiumi, 8 Kabaa-Athi.

2.2.2 Distribution and infestation levels of Tuta absoluta

Surveys of the distribution of *T. absoluta* in Eastern Africa, covering 226 different locations, were conducted between January 2016 and October 2018. In Kenya, 96 locations were sampled, while 53, 31, and 46 locations were sampled in Sudan, Tanzania, and Uganda respectively. The intention of the surveys was to determine the distribution of *T. absoluta* across the four Eastern Africa countries. No preference for selection was allocated to any of the countries, and locations sampled in each country/district/state were not predetermined but based on the presence of farming activities involving tomato plants. Within each sampled location, tomato plants grown under open-field and/or under greenhouse conditions were sampled for *T. absoluta*. Due to the tendency of *T. absoluta* to utilize some crops and plants other than tomato, we also sampled a few other known host plants of the pest such as eggplant, potato, sweet pepper, and black nightshade (*Solanum nigrum* L.). Prior to the sampling at all locations, permissions were obtained from the farmers, landowners, or appropriate authorities in each instance, and then, visual examination of the host plants for *T. absoluta* was conducted.

At all locations, the following indices were subsequently used to determine the presence of *T. absoluta*: the presence of immature stages of the moth (larvae and pupae), adult moths (collected by sex pheromone/sticky traps), and the mines, specific to *T. absoluta* herbivory. Location geographic information such as coordinates, and altitudes were obtained using a Gamin ETrex 10 handheld GPS or Google Earth.

To estimate the infestation levels of *T. absoluta*, five replicates of a $1m^2$ quadrat were randomly placed over tomato (cv. Money maker) plants in two locations (growers plot) each of the four selected counties of Kenya (Fig. 2.1) from the beginning of a growing season (March 2018) to two-weeks prior to fruit harvesting (June 2018) (Fig. 2.1). The quadrats defined an area on the plants from which 50 leaves were then selected and examined for the presence of *T. absoluta* mines (see Desneux et al., 2010 for description) and five tomato fruits were sampled for the presence of larvae. Sampling was conducted every fortnight at each location. At all eight plots, the farmers applied insecticides to the plants every 5 or 7 days.

2.2.3 Livelihood survey

Two hundred farms that produced tomatoes (50 each in Kajiado, Kwale, Machakos, and Taita Taveta counties) in Kenya were selected. These farms were selected based on tomato farming activities and by randomization from a list of locations provided by agricultural extension officers in each of the four counties. At each of the locations/farms selected, one farmer in the same working group was randomly selected and interviewed (orally using a questionnaire). The interviews were conducted in the local language (Kiswahili) and with the help of a local extension officer appointed by the International Center of Insect Physiology and Ecology in Kenya. The questionnaire, based on that of Shackleton et al. (2017) albeit with modifications, provided information on the farmer's knowledge and perceptions of the introduction and spread of *T. absoluta* in their respective counties. It also allowed for the collection of information on the perceptions and knowledge of the impacts of *T. absoluta*, with a focus on production costs of tomato as well as the indigenous management, wants and needs regarding the management of *T. absoluta*. To do this (i.e. to assess the farmers knowledge and perceptions of both *T. absoluta* and other stressors – pests and diseases), we recorded the descriptions of each stressor provided by each farmer and then sampled their farms to identify the stressors. Following our identification of the stressors, we presented them to the farmers and thus validated their previous descriptions.

2.2.4 Statistical analysis

Chi-square analysis was used to assess the independence of the categorical data. For the numerical data sets Shapiro and Wilk's and Bartlett's tests were used in testing the normality and homoscedasticity, respectively. Subsequently, data was subjected to One-Way Analysis of Variance (ANOVA) or a generalized linear model with a negative binomial distribution and log link function (in instances were assumptions of parametric tests were not met) to assess differences in responses and insect densities from the four counties. When significant differences were detected, in each of the cases, data was then subjected to Tukey's test. The proportion data was analyzed with SPPS 23.1, while the numerical data were analyzed in R 3.5.1 (R core team, 2018). Monetary values are reported in USD (US dollar) and KSH (Kenya shillings), with 1 USD equivalent to 100 KSH.

2.3 Results

2.3.1 Distribution and infestation levels of Tuta absoluta

Tuta absoluta was recorded in all 226 locations sampled in Eastern Africa (Fig. 2.2). Mines, which were apparent on tomato leaves, were the most prevalent sign of the pest. Adults were easily collected with pheromone/sticky traps. Eggs and pupae of the moth were also observed at all locations. In Kenya, from the first detection site, Mpeketoni (2° 23'23.028"S40°41'44.952"E) in Lamu county, *T. absoluta* has now spread over 1000 km since 2014. Similarly, in Sudan, Tanzania, and Uganda, it has spread about 600, 850, and 900 km respectively since its first report. Overall, in the four counties of Kenya, 32 of 50 tomato leaves per m^2 were infested in one growing season. The highest number of infested leaves was recorded at Taita Taveta albeit not significantly different from Kajiado and Machakos (Fig. 2.3). Almost half, (Mean ±SD 2.3 ± 0.89 fruit/m^2) the number of fruits sampled had at least one *T. absoluta* larva present. However, the number of infested fruits was low in Kwale County, with an average of one infested fruit per m^2 (Fig. 2.3).
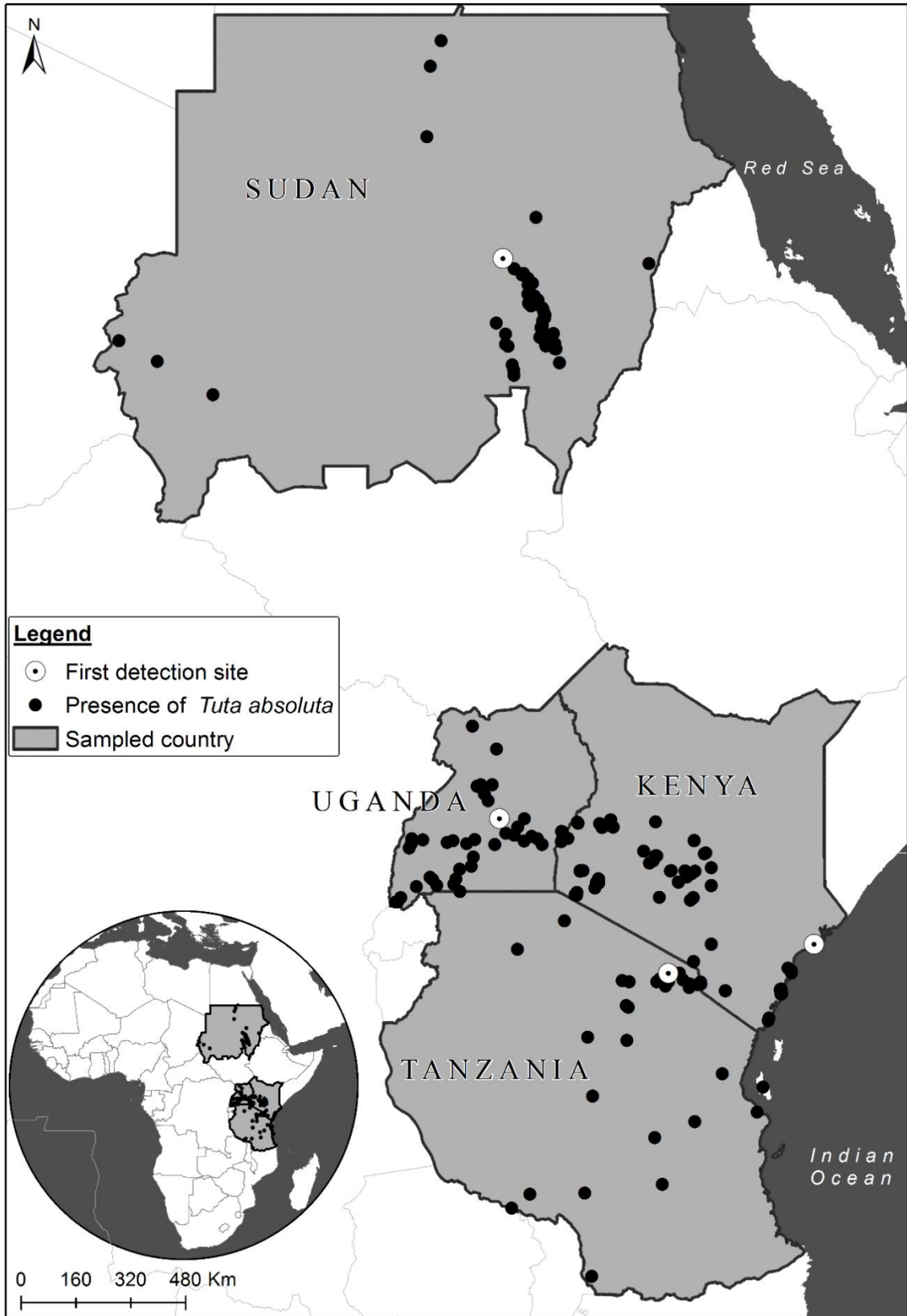
Figure 2.2 Distribution of *Tuta absoluta* in four Eastern African countries as of October 2018.
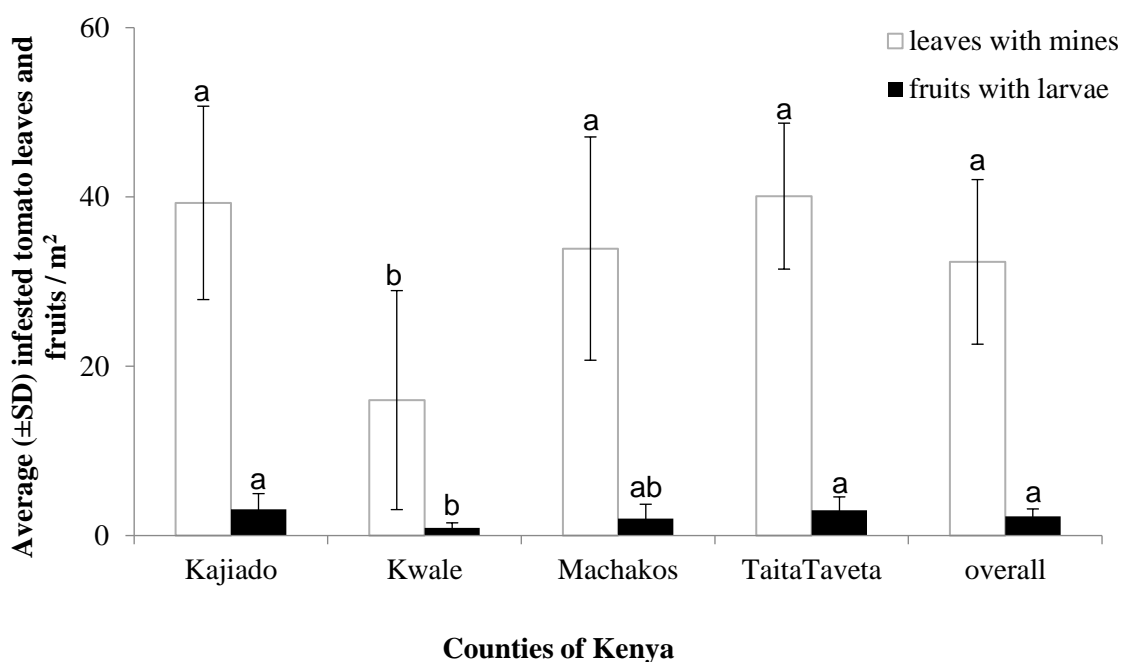
Figure 2.3 *Tuta absoluta* infested leaves (GLM, $\chi^2_3 = 23.619$; $P = < 0.0001$) and fruits (GLM, $\chi^2_3 = 15.216$; $P = 0.002$) of tomato per m^2 in one growing season, in the four counties of Kenya as of October 2018. For each plant parameter (fruits and leaves), means with different letters are significantly different (Tukey's HSD test, $P < 0.05$).

2.3.2 Livelihood survey

2.3.2.1 Respondents demographics

Overall, most of the respondents were male (89%). This was the case in each of the four study counties (Table 2.1). Half (50 %) of the population of the respondents had a certain degree of education, but most (70%) had only attended primary school. This trend was observed in all four counties. Respondent age and household size (Mean ± SD) were 29.20 ± 0.47 years and 5.73 ± 0.52 people and did not differ across the counties. Farm sizes of the respondents were significantly different across the counties. A significantly higher proportion (~67%) of respondents had farms with only tomato compared with those (~ 33%) with both tomato and maize (Table 2.1). Farmers with both crops (tomato and maize) had them planted within the same rows.

Table 2.1 Socio-demographic characteristics (Mean ± SD, or percentage) of the respondents across four sampled counties in Kenya

	Kajiado	Kwale	Machakos	Taita Taveta	Overall sample	Statistic
Age (years)	28.72 ± 0.07a	30.45 ± 6.67a	28.76 ± 5.37a	29.20 ± 5.59a	29.28±0.47	$F = 0.79$; $P = 0.499$
Household size	6.00 ± 2.39a	5.96 ± 1.80a	5.38 ± 1.623a	5.60 ± 1.67a	5.73 ±0.52	$F = 1.19$; $P = 0.313$
Gender						
% Male	94	98	84	78	88.5	$\chi^2 = 12.33$; $P = 0.006$
% Female	6	2	16	22	11.5	
Level of Education (%)						
% Primary school	66	78	58	80	70	$\chi^2 = 7.56$; $P = 0.056$
% Secondary school	34	22	42	20	30	
Farm size (ha)	0.56 ± 0.55a	0.97 ± 0.54b	1.08 ± 0.55b	0.93 ± 0.42b	0.89 ± 0.20	$F = 0.86$; $P = 0.042$
Farm produce						
Tomato	32	100	68	70	67.34	$\chi^2 = 12.03$; $P < 0.001$
Tomato+Maize	68	0	32	30	32.66	

Means within the same rows with different letter indicate significantly different (Tukey's test $P < 0.05$)

2.3.2.2 Local knowledge of invasive arthropods and perceptions of the introduction and spread of Tuta absoluta

About 61% of the respondents claimed they had no knowledge of IAS, but the rest had knowledge prior to our interview/discussions. The highest percentage of respondents with prior knowledge was recorded in Machakos county (Fig. 2.4); Kajiado county had the highest percentage of respondents who had no knowledge of IAS (Fig. 2.4). The respondents with IAS knowledge identified three species, *T. absoluta*, Fall Armyworm (*Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae)), and Whiteflies (Hemiptera: Aleyrodidae) (not identified to species level), as invasive, which was confirmed to be present, in their counties. Overall, *T. absoluta* and *S. frugiperda* were highlighted significantly more frequently than whiteflies as problematic (Fig. 2.4).
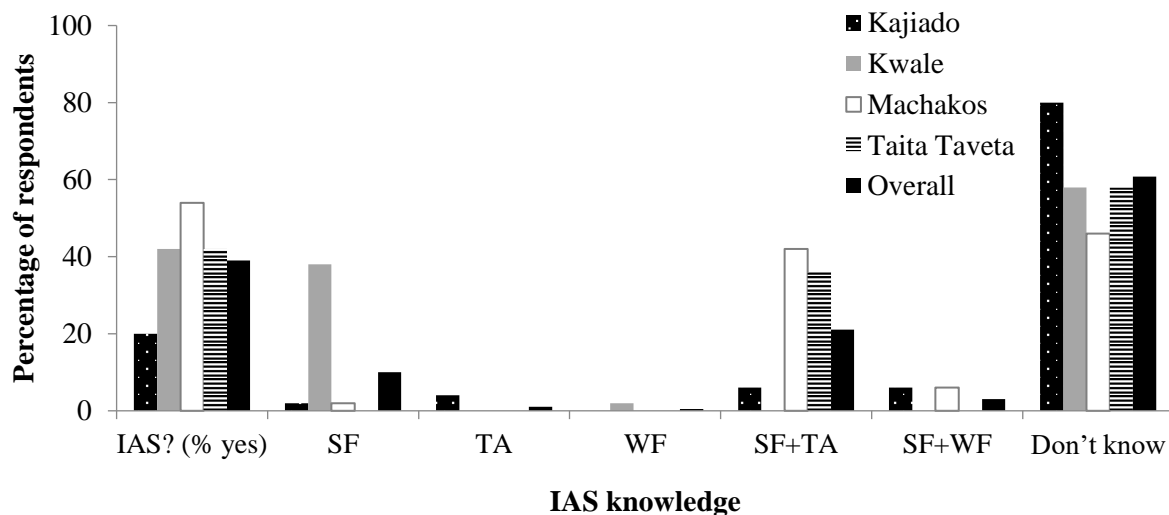
Figure 2.4 Respondents knowledge of ($\chi^2 = 12.55$; $P = 0.006$), and the occurrence ($\chi^2 = 99.46$; $P < 0.001$) of IAS in their counties. IAS? (% yes) indicates the percentage of respondents who had prior knowledge of arthropod invasive species. SF, TA, WF, SF+TA, and SF+WF indicate *Spodoptera frugiperda*, *Tuta absoluta*, Whiteflies, *Spodoptera frugiperda* and *T. absoluta*, and *Spodoptera frugiperda* and Whiteflies respectively. Note that there are a number of Whitefly species in Kenya, and while the presence of *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae) was confirmed, there are others which were not identified.

The majority (91%) of the respondents had good knowledge of the first detection (2014 and 2015) of *T. absoluta* in Kenya. However, a few highlighted 2011, 2013, 2016, and some were not sure (Fig. 2.5).
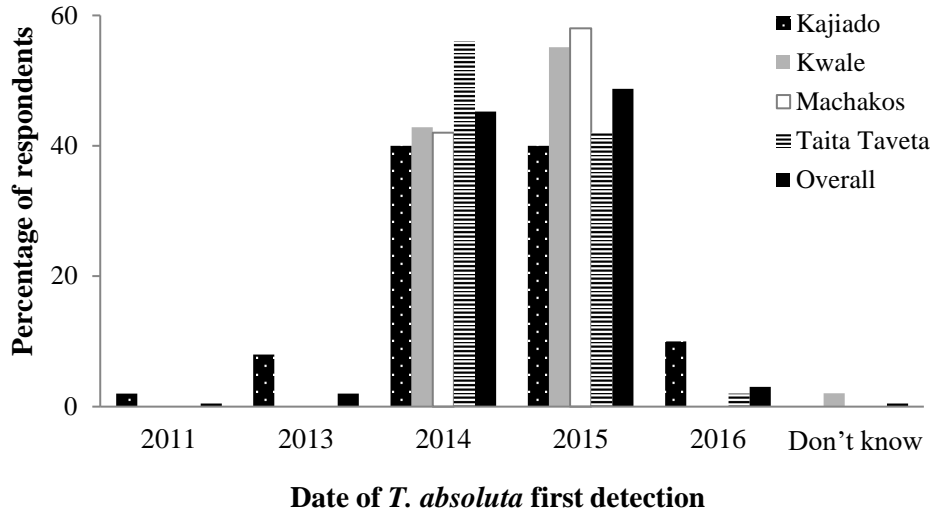
Figure 2.5 Perceptions of respondents regarding the date of the first detection of *Tuta absoluta* ($\chi^2 = 33.81$; $P = 0.004$).

Subsequently, they highlighted natural means such as wind and the flight ability of *T. absoluta* (54.5%), anthropogenic means such as the transportation of infested fruits and seedlings (10%), and a combination of both (35.5%) as the fundamental drivers facilitating the spread of *T. absoluta* in Kenya (Table 2.2). Almost all (97%) the respondents highlighted an increase in the range of the pest in the country (Table 2.2) as a concern.

Table 2.2 Frequencies (as percentage) of respondents regarding the spread pathways of *Tuta absoluta*

	Kajiado	Kwale	Machakos	Taita Taveta	Overall sample	Statistics
Pathways						
Wind (W)	42	66	50	38	49	$\chi^2 = 88.85$; $P < 0.001$
W+IS	0	0	0	8	2	
IF	2	0	4	6	3	
IF+IS	4	0	4	8	4	
IS	0	0	10	2	3	
PF	6	6	8	2	5.5	
W+PF	0	2	6	18	6.5	
W+IS	14	4	0	0	4.5	
W+IF	8	0	0	6	3.5	
W+IF+IS	24	22	18	12	19	
Spreading?						
(% yes)	100	100	100	100	100	$\chi^2 = 0.00$; $P = 1.000$

IS = Infested seedlings; IF = Infested fruits; PF = Pest flight – indicating the innate capacity of *Tuta absoluta* to fly from one location to another.

2.3.2.3 Socio-ecological stressors

Several socio-ecological stressors were highlighted and considered as significant threats to indigenous livelihoods in Kenya (Table 2.3). Invasive arthropods, such as *T. absoluta* and *S. frugiperda*, water shortage, and tomato plant disease such as *Phytophthora infestans*, and *Alternaria solani* were highlighted (Table 2.3). In all four counties, *T. absoluta* was, however, ranked both as the worst invasive arthropod pest and socio-ecological stressor (Table 2.3; Fig. 2.6); water shortage, *S. frugiperda*, Whiteflies, *P. infestans*, and *A. solani* were also highlighted as significant threats (in order of importance).

Table 2.2 Frequencies (as percentage) of respondents stating different socio-ecological stressors of local livelihoods in their counties

	Kajiado	Kwale	Machakos	Taita Taveta	Overall sample	Statistics
Water shortage	76	0	90	100	66.5	$\chi^2 = 46.44$; $P < 0.001$
Invasive arthropods	100	100	100	100	100	
Fungi						
P. infestans	0	0	0	48	12	
A. solani	4	22	20	0	11.5	
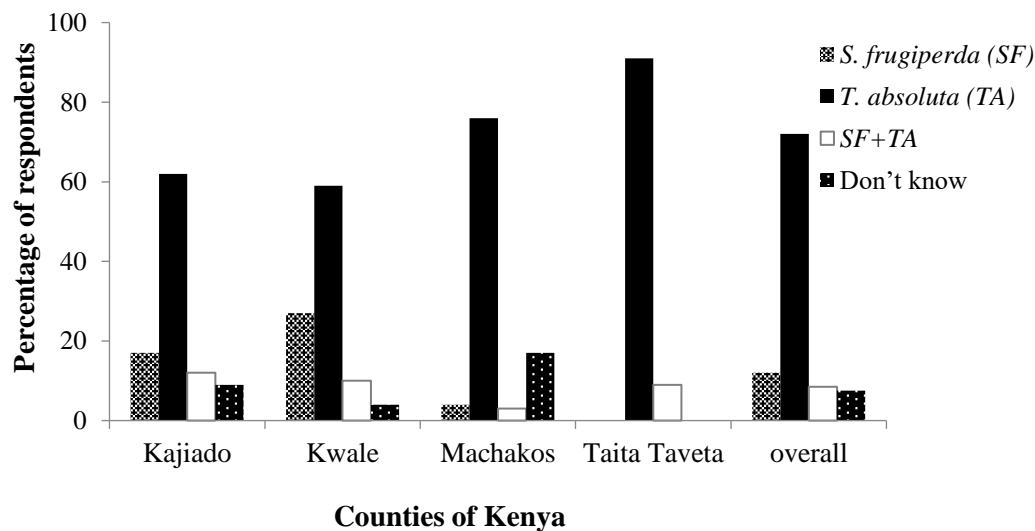
Figure 2.6 Perception of respondents ranking the two major invasive arthropods in their villages ($\chi^2 = 24.33$; $P = 0.004$).

In all four counties, 72% of the respondents highlighted *T. absoluta* as the worst socio-ecological stressor. This was significantly different from the respondents (12%) who thought

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S. frugiperda was the worst. However, a few (8.5%) categorized the impact of both *T. absoluta* and *S. frugiperda* as equivalent, while others (7.5%) where undecided (Fig. 2.6).

2.3.2.4 Impact of Tuta absoluta

All respondents highlighted several negative direct and indirect impacts of *T. absoluta* on their households and counties, respectively (Table 2.4; Box 2.1). Respondents, (50%), (49%), (50%), and (50%), in Kajiado, Kwale, Machakos, and Taita Taveta counties respectively, highlighted losses in livelihood and the economy with an increase in the cost of tomato production. The same percentage of respondents in each of the counties (except Kwale with 51%), highlighted household monetary losses due to the reduction in tomato yield which subsequently resulted to indirect impacts such as increased debt incurred from pesticide purchases, as well as reductions in daily meal frequencies. In combination with monetary losses, a few respondents (~10%) highlighted an increased time spent in spraying pesticides (Table 2.4).

Table 2.3 Respondents (%) perception of the impact of *Tuta absoluta* in some of the invaded areas of Kenya

	Kajiado	Kwale	Machakos	Taita Taveta	Overall sample	Statistic
County impact						
Economic loss (EL)	6	4	13	8	7.75	$\chi^2 = 91.163; P < 0.001$
EL + LL	0	24	15	5	11	
ICTP + LL	29	21	0	12	15.5	
ICTP	15	0	22	25	15.5	
Household impact						
Monetary loss (ML)	14	0	8	0	5.5	$\chi^2 = 133.89; P < 0.001$
ML+ RFM+ debt	0	10	0	9	4.75	
ML + debt	7	19	35	7	17	
ML + IEP	0	9	7	23	9.75	
ML + RFM	29	13	0	11	13.25	

LL, ICTP, RFM, and IEP, indicate livelihood loss, increased cost of tomato production, reduction in the frequency of meals, and increased exposure to pesticides.

Box 2.1 Selected quotes, albeit re-phrased, of respondents highlighting the local perception and devastating effect of *Tuta absoluta* in Kenya
1 "With my many years of farming experience, it is easy to say that *T. absoluta* is the worst pest of tomato I have seen. Francis Meitamei Kajiado County."   2 "In 2015, when I first detected *T. absoluta* in my farm, I used several different kinds of pesticides, but none was effective. It was a bad year." Charo Juma Kimala Kwale County."   3. "A research institute (name withheld) is responsible for the introduction and spread of *T. absoluta* in Kenya. John Mwaura Kajiado County"   4. "I am now farming in just one of my four farms because of the losses incurred in previous farming seasons. Morris Mwakera Taita Taveta County"   5. "Before, I earned over 80,000 KSH (~ USD 800) at the end of every farming season. Now, and because of the cost of pesticides, if I get 30,000 KSH, then, it is a good season. Caroline Ndetei Maweo Taita Taveta County"   6 "If you do not spray your farm, after a few days, densities of the pest could increase as before. Ann Kaluki Mwelu Machakos County"

2.3.2.5 Management of Tuta absoluta

All respondents in each of the four different counties highlighted the use of chemical pesticides as the major control strategy for managing *T. absoluta* (Fig. 2.7A). A few respondents (~5%), only in Machakos and Taita Taveta counties, highlighted the use of a pheromone/sticky traps (manufactured and distributed by Kenya Biologics), with pesticides (Fig. 2.7A). The frequency of pesticide application, however, varied across the counties and differed significantly from the frequencies prior to the arrival of *T. absoluta* (Fig. 2.7B and 2.7C). The invasion of *T. absoluta* has more than doubled the frequency. The spray frequency interval of 5 -7 days following previous applications was most prevalent and differed significantly from prior prevalent frequency regimes (30 days interval) (Fig. 2.7D). The highest frequencies were recorded in Kajiado and Taita Taveta (Fig. 2.7C).
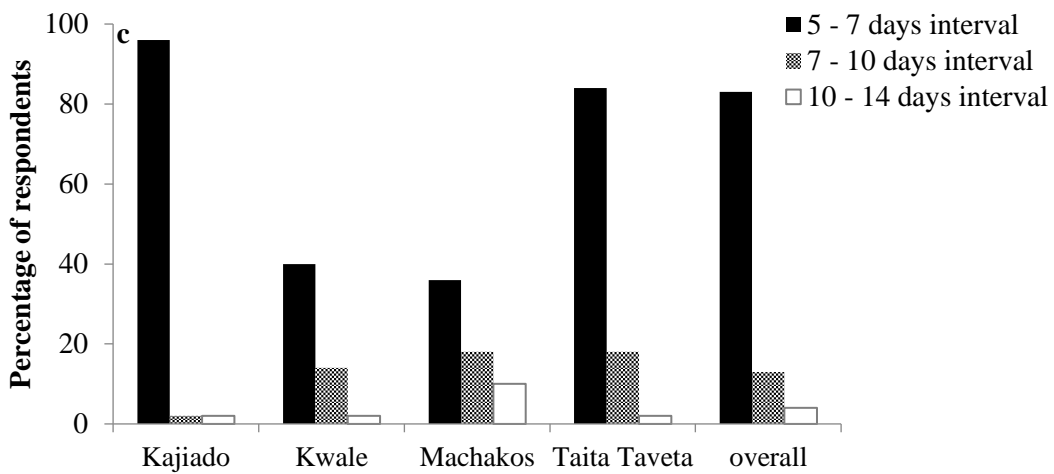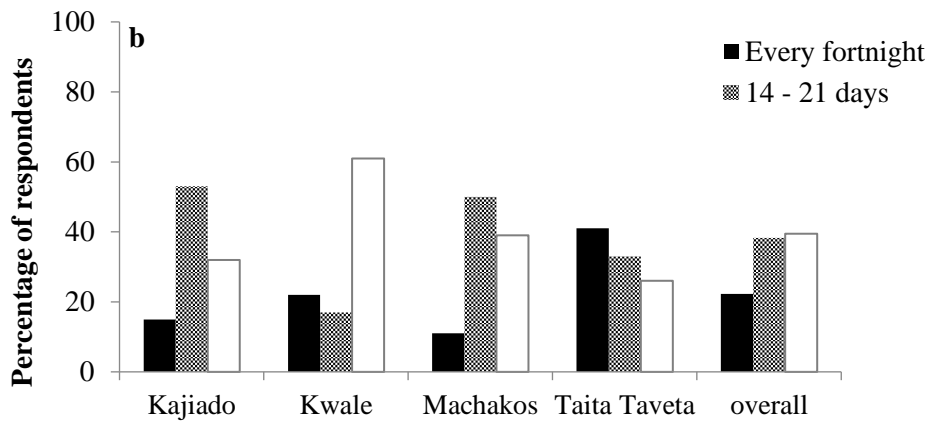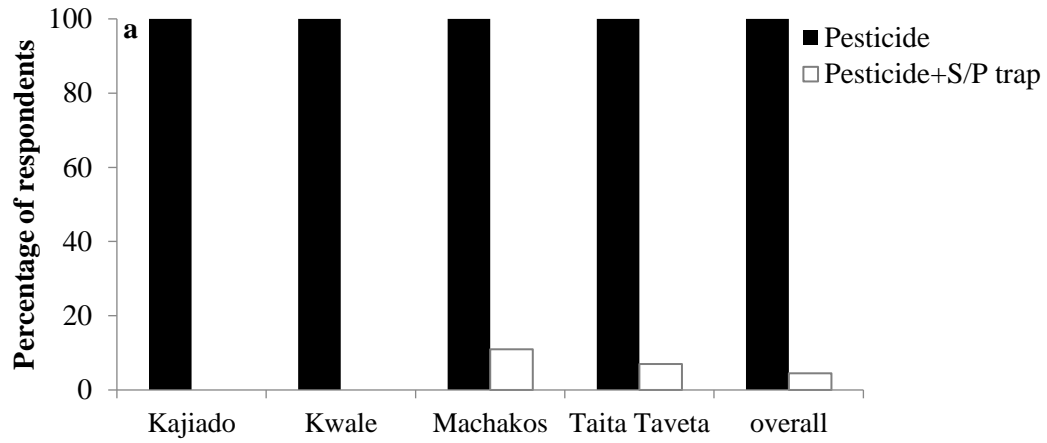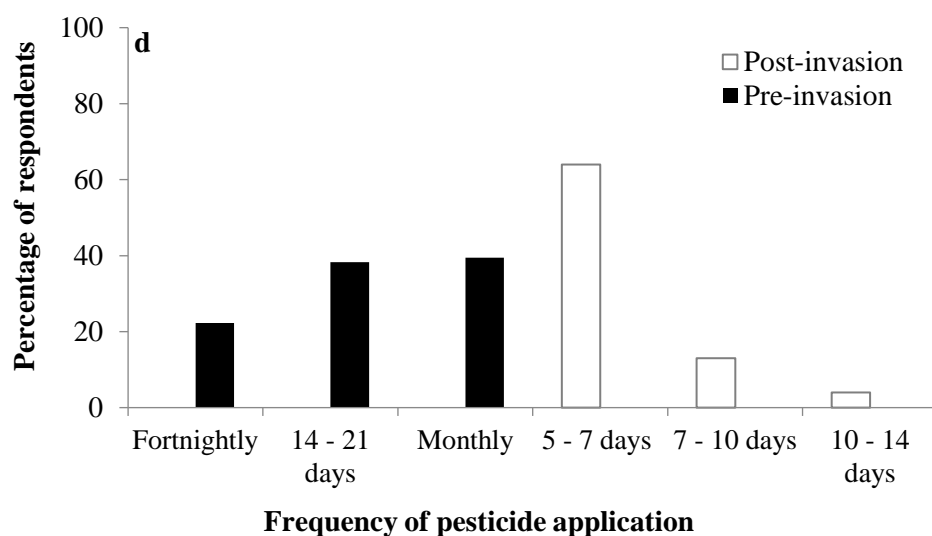
Figure 2.7 Respondents estimation of the (A) different control strategies used in managing the impact of *Tuta absoluta* ($\chi^2 = 101.53$; $P < 0.001$), and frequency (days interval) of pesticide application (B) prior ($\chi^2 = 0.07$; $P = 0.696$) and, (C) post invasion of *Tuta absoluta* ($\chi^2 = 14.423$; $P = 0.025$), and (D) change in the frequency of pesticide application. S/P trap indicates a combination of a sticky and pheromone trap ($\chi^2 = 136.97$; $P < 0.001$).

All respondents had no knowledge of biological control. Following several rounds of discussions some of the respondents (30% and 28 % in Kwale and Taita Taveta counties respectively) expressed their satisfaction with our proposed integrated pest management approach, encompassing the use of a newly imported parasitoid. However, and significantly different from the above 30%, ($\chi^2 = 87.79$; $P < 0.001$), the majority of the respondents (70%) were undecided, i.e. they were not sure if the proposed intervention would be favorable. The use of effective pesticides was considered by all respondents as the best management strategy against *T. absoluta* (Fig. 2.8).
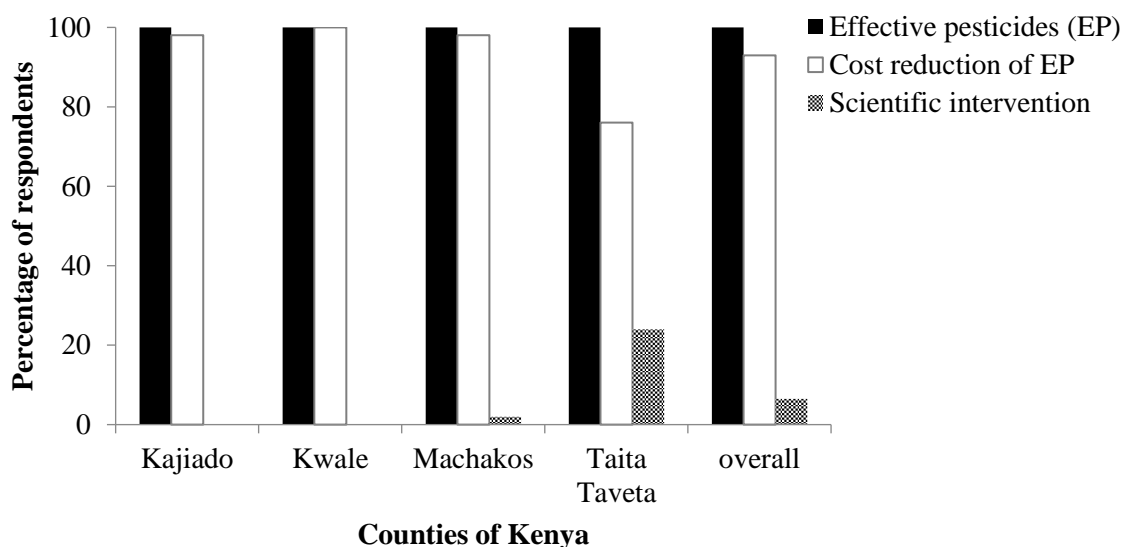
Figure 2.8 Respondents perception of the best management options and wants for the control of *Tuta absoluta* ($\chi^2 = 142.16$; $P < 0.001$). Scientific intervention was referred to (by the farmers) as the transfer of useful research findings from scientific institutions to small-scale farmers for the control of the pest.

2.3.2.6 Cost of tomato production pre - and - post -Tuta absoluta invasion

The responses of the people interviewed showed that *T. absoluta* has more than doubled the cost of tomato production. Prior to the invasion of *T. absoluta*, the cost per growing season (USD $450) of tomato production, across different tomato agro-ecosystems in the counties of Kenya, did not differ (F= 0.02; *P* = 0.997). However, following the invasion of the pest, the average management cost (USD $1062) differed significantly (F= 13.71; *P* < 0.001) from the previous average management costs in the four counties (Table 2.5).

Table 2.4 Average cost (USD) of tomato production, in one growing season, prior and after the arrival of *Tuta absoluta* in Kenya

	Kajiado	Kwale	Machakos	Taita Taveta	Overall sample	Statistics
Pre-invasion	450	460	440	450	450	$\chi^2 = 26.087$; $P < 0.001$
Post-invasion	1031	1049	1037	1132	1062	

43

2.4 Discussion

Although *T. absoluta* is a recent invader in Eastern Africa, it has become widespread in a relatively short time. This was supported with the response by the majority of the villagers (respondents) in Kenya who stated that it was first seen in the country in 2015 but is now widespread (our sampling data). Evidently, *T. absoluta* has expanded its distribution range, since its first detection, in each of the four surveyed countries, spreading over 1000, 600, 850, and 900 km in Kenya, Sudan, Tanzania, and Uganda, respectively. The infestation level, derived from leaves and fruits, of the pest in four counties of Kenya showed that *T. absoluta* is distributed in high abundance across the country. Fruit is routinely discarded by the farmers during harvesting as a result of the rot induced by opportunistic pathogens which infested the fruits via the galleries created by *T. absoluta* larvae. Although this study did not estimate densities at Naivasha (0°43'0.192"S36°25'54.552"E) in Nakuru county of Kenya, the abundance of leaf mines indicating the presence of larvae of the pest, observed by visual examination of some of the different host plants, notably, tomato, was serious. In one of our two visits to this county in July 2018, tomato plants, in over 10 greenhouses (~ 50 x 65 x 15 meters: length: width: height), were removed and discarded due the affected health of the plants induced by high infestation levels of the pest. Here, the farmers at Naivasha emphasized that they normally incur such losses when the pesticides applied against the pests were not effective. These findings and the testaments of the respondents in this study indicates that *T. absoluta* has established and widely distributed in high populations in high populations densities in Eastern Africa. The implications of these findings are serious, as recorded in the livelihood surveys, and validates previous studies reporting the rapid rate of the spread and climatic suitability of *T. absoluta* in the new and potential areas of its invasion (Desneux et al., 2010, 2011; Tonnang et al., 2015, see Santana et al., 2019 for recent review).

The impacts of IAS on humans increase following invasion, with increasing effects on well-being and cost for livelihoods (Bennett and van Sittert, 2019; Pejchar and Mooney, 2009; Shackleton et al., 2017; Udo et al., 2019). The impact of *T. absoluta* in Kenya has resulted in serious losses both in indigenous tomato-dependent livelihoods and tomato production. It has also impacted negatively on indigenous well-being and intensified the effects of the socio-ecological stressors of tomato production in the country. Here, the villagers, although highlighting water shortage, *P. infestans*, *A. solani*, whiteflies, and *S. frugiperda*, ranked *T. absoluta* as the worst stressor plaguing tomato-dependent livelihoods in their communities.

Increasing evidence suggests that the impact of IAS in rural households is more severe than in urban and sub-urban households, as rural dwellers are more reliant on natural resources and provisioning ecosystem services for livelihoods (Shackleton et al., 2007; Shackleton et al., 2019). In this context, and in addition to livelihood losses and the increase in the cost of tomato production and purchases in their respective counties, the villagers highlighted several indirect household impacts of *T. absoluta*, including rising debt and reductions in meal frequencies due to monetary losses incurred. It is noteworthy that similar indirect impacts of *T. absoluta* on indigenous households, reported here, have been recorded recently in West Africa (Aigbedion-Atalor et al., unpublished data). This clearly indicates that the impacts of IAS are not limited to ecological consequences alone, and that socio-ecological impacts are as serious as the ecological impacts.

Although a few villagers combined the use of pesticides with pheromone and sticky traps, the use of chemical pesticides was widespread and, currently, it is the most common control strategy. Pesticide use was considered as the most effective pest control method, providing some relief of the pest's pressure. However, the change in the frequency of pesticide application, following the invasion of *T. absoluta*, recorded in this study is concerning. It is not unlikely that the current frequency of application will increase overtime due to the possibility of resistance to several of the pesticides used (see. Guedes et al., 2012; 2019). The current significantly increased cost of tomato production is a direct result of the increase in pesticide use. Several of the villagers ranked the current monetary pressure triggered by *T. absoluta* in tomato production as the worst they have experienced in their years of farming. This has further triggered increases in the cost of tomato fruit purchase countrywide.

In the context of the five domains of sustainable livelihood framework (Chambers and Conway, 1992; Scoones, 1998), the majority of our data suggested that *T. absoluta* has impacted all five domains in Eastern Africa by: (1) acting as a shock and stress (first domain), (2) eroding capital (second domain), (3) increasing its distribution range and impact due to porous sub-regional borders (third domain), (4) inducing yield loss in tomato (fourth domain), and (5) increasing the cost of tomato production and human vulnerability – exposure to chemical pesticides (fifth domain).

Shackleton et al. (2019), in a recent review, underscored the role of IAS in shaping local sustainable livelihoods and human well-being. The authors clearly showed that the interplay between IAS and indigenous livelihoods is a highly complex matter. Highlighting the detrimental effects of IAS, which encompass increased vulnerability within socio-ecological systems, the aforementioned authors noted that impacts of IAS may be variable, and may also be evident between demographics and gender, especially around health and safety issues (de Neergaard et al., 2005; Ngorima and Shackleton, 2019; Norgaard, 2007). Furthermore, they asserted that some IAS may induce serious changes (directly, indirectly, or both) in human health and safety and reduce the cultural value of landscapes. While we do not have any evidence suggesting demographic or gender differentiation in the impact of *T. absoluta* in Eastern Africa, it is prudent to state that *T. absoluta* has induced significant changes in the cultural perception of tomato production and human well-being in Eastern Africa.

In conclusion, the classical example of successful biological control of IAS in Africa, showing the control of *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae), depicts the importance of biological control strategies against IAS on the continent (Neuenschwander, 2001). Therefore, the promotion of biological control, encompassing the use of parasitoids, predators, and pathogens, both alone and in combination; but in an integrated approach with other control strategies such as the pheromone and sticky traps currently being used by farmers against *T. absoluta* in the sub-region is recommended. Although respondents were sceptical of this approach, implementing such a program may be challenging. Clearly, there is a need for both regional and sub-regional concerted alliances for the control of *T. absoluta* in Africa, notably, in Eastern Africa. Further studies on the socio-ecological dimensions of *T. absoluta* in other parts of Eastern Africa not covered in this study and beyond, where the socio-ecological impact of the pest is alarming, are warranted.

CHAPTER 3

Host stage preference and effects on the fitness of *Dolichogenidea gelechiidivoris* (Hymenoptera: Braconidae), a potential biological control parasitoid of *Tuta absoluta* in Africa*

3.1 Introduction

In novel ranges, alien species are often free or released from top-down control by natural enemies such as parasitoids, predators, and pathogens which are crucial for suppressing their populations in the native range (Keane and Crawley, 2002). This is the known as the enemy release hypothesis. Fundamentally, the enemy release hypothesis also referred to as enemy escape or escape-from-enemy hypothesis, predicts that alien species introduced in novel ranges will experience reduced impacts from natural enemies (parasitoids, predators, and pathogens), due to the escape from enemy regulation, resulting in increased population growth and distribution (Blumenthal, 2006; Keane and Crawley, 2002; Liu and Stiling, 2006). This theory is largely based on the assumption that natural enemies are important biotic factors in regulating populations, thus representing the theoretical crux of classical biological control which seeks to reduce the population and impacts of alien species in novel ranges through the importation of effective natural enemies from native ranges (Keane and Crawley, 2002; Mills, 2005; Müller-Schärer et al., 2004). However, prior to the release of an exotic natural enemy in a new environment, pre-release evaluations of the attributes (e.g., host specificity, host acceptability and suitability) of the potential biological control agent need to be assessed as they represent crucial aspects of any classical biological control (Kuhlman et al., 2006; Sands and Van Driesche, 2004; van Lenteren et al., 2006). Here, under laboratory conditions, aspects of the biology of *Dolichogenidea gelechiidivoris* Marsh (Hymenoptera: Braconidae), including egg maturation dynamics, host stage preference, acceptability, and suitability, with *T. absoluta* as the host are documented. As a part of this new classical biological control against *T. absoluta*, the results of this study will form a baseline for the considerations of the release of *D. gelechiidivoris* in the African continent and beyond.

3.2 Materials and Methods

3.2.1 Host plant

Tomato plants (cv. Money maker) were grown in plastic pots (10.5 cm diameter and 14.5 cm high) containing approximately 2.5 kg of Peat compost. One hundred gram of NPK (Nitrogen, Phosphorous and Potassium) fertilizer was applied to each pot at planting, with a density of two plants per pot in a screen house at the international centre of Insect Physiology and Ecology (*icipe*) (1°17'8.844"S36°49'12.108"E) in Nairobi, Kenya. Two-week-old potted plants were supplied periodically and used in all the experiments.

3.2.2 Insects

3.2.2.1 Tuta absoluta *colony*

The initial colony of *T. absoluta* used in this study was collected from tomato farms in Isiolo County (0° 21' 20.2896" N 37° 34' 59.898" E, with elevation ≈ 300 msl) of Kenya in 2015. In a controlled environment (~26°C ± 4 (range: 24 to 29°C), 60 ± 5% RH and photoperiod of 12:12 L:D), adults were reared in Perspex cages (65 cm x 45 cm x 45 cm) each containing four potted tomato plants. Little streaks of honey solution (80% honey) were placed *ad libitum* to the top sides of each cage as food source for adults. To complement the genomic pool of the established laboratory colony, different life stages (eggs, larvae, pupae, and adults) of the moth were collected from several tomato fields and greenhouses, across 25 different counties of Kenya during 2017 and 2018 (see Table 3.1).

Table 3.1 Counties of Kenya where *Tuta absoluta* was collected to maintain the genomic pool of the established laboratory colony

County	GPS coordinates	Number of sites sampled
Busia	0° 27' 52.272" N 34° 6' 7.74" E	5
Embu	0° 32' 16.8" S 37° 27' 15.588" E	5
Homa Bay	0° 31' 37.848" S 34° 27' 20.556" E	3
Kajiado	1° 50' 30.984" S 36° 47' 21.3648" E	14
Kakamega	0° 16' 56.784" N 34° 45' 15.228" E	2
Kilifi	3° 38' 1.32" S 39° 50' 59.46" E	4
Kirinyaga	0° 28' 15.276" S 37° 19' 51.4956" E	1
Kisii	0° 40' 27.228" S 34° 46' 14.664" E	1
Kitui	1° 21' 54.036" S 38° 0' 41.652" E	2
Kwale	4° 10' 31.116" S 39° 27' 11.952" E	7
Laikipia	0° 16' 56.784" N 36° 47' 30.9516" E	3
Limuru	1° 6' 33.66" S 36° 38' 35.592" E	11
Machakos	1° 31' 6.348" S 37° 16' 0.8364" E	13
Makueni	1° 48' 22.248" S 37° 37' 16.9248" E	2
Meru	0° 2' 47.004" N 37° 39' 9.8928" E	8
Migori	1° 3' 48.924" S 34° 28' 22.5084" E	2
Mwea	1° 41' 47.04" S 37° 25' 2.712" E	5
Nakuru	0° 16' 53.364" S 36° 4' 42.3084" E	15
Narok	1° 5' 16.692" S 35° 52' 23.16" E	3
Nyandarua	0° 32' 26.232" S 36° 36' 36.2484" E	2
Nyeri	0° 25' 16.14" S 36° 56' 57.8724" E	2
Siaya	0° 3' 44.568" N 34° 17' 20.616" E	1
Subukia	0° 2' 2.472" S 36° 9' 50.004" E	1
Taita Taveta	3° 23' 31.92" S 37° 40' 26.832" E	12
Uasin Gishu	0° 28' 18.624" N 35° 13' 12.2088" E	1

3.2.2.2 Dolichogenidea gelechiidivoris *colony*

A batch of 200 cocoons of *D. gelechiidivoris* was received from the International Potato Centre (CIP) in Peru (16°57'36.252"N96°28'32.052"W) at the quarantine facility of *icipe* in March 2017. The cocoons were placed in a single sleeved Perspex cage (30 x 30 x 30 cm), in the same environmental conditions in 3.2.2.1 (26 ± 4°C (range: 24 to 29°C), 60 ± 5% RH and photoperiod of 12:12 L:D) until wasp emergence. Wasps were transferred into another single sleeved Perspex cage (65 x 45 x 45 cm) containing several batches of mixed instars of *T.*

absoluta on four potted tomato plants for 48 h. New batches of *T. absoluta* larvae (as described above) were offered to the parasitoids every 48 h. Newly emerged wasps were fed in the same manner as above. This procedure ensured the establishment of our laboratory colony of *D. gelechiidivoris*; herein 10 generations of the host were used for mass rearing the parasitoid prior to the start of the experiments. All experiments with the parasitoid were conducted in the quarantine unit, a level two biocontainment laboratory, at the insectary complex of *icipe*.

3.2.3 Host instar preference and acceptability

Choice and no-choice tests were conducted to determine the host instars preference and acceptability of *D. gelechiidivoris* females. In the choice tests, and under the same physical conditions in section 3.2.2.1, eight mated naive *D. gelechiidivoris* females (< 24 h post-eclosion) were released in a single sleeved Perspex cage (65 x 45 x 45 cm) containing four potted tomato plants (four leaflets per plant) each with one of the four larval instars (40 larvae/host instar) of *T. absoluta* (i.e. a ratio of 1 parasitoid to 20 host larvae) for 24 h. The experiment was replicated 12 times, with each potted plant assuming a position in the cage different from the prior replicate. The parasitoids were fed with honey solution (80%) as in 3.2.2.1, and each replicate had a new set of both plants and parasitoids as described above. After 24 h, the potted plants were removed from the cages and then 10 larvae each of the four instars (i.e. a total of 40 larvae per replicate) were removed from the leaf mines using a scalpel and a camel hairbrush. The larvae were then placed individually in a drop of phosphate buffer solution on a Petri dish (8.5 cm diameter) and dissected under a Leica EZ4D stereomicroscope (Leica Microsystems Switzerland Ltd, 2007). The numbers of parasitized *T. absoluta* for the different instar stages were recorded. The potted plants each with the remaining 30 *T. absoluta* larvae were transferred individually into a different single sleeved Perspex cage (30 x 30 x 30 cm) for host and parasitoids development (the number of cocoons formed, emerged wasp, sex ratio and developmental time). In the no-choice tests, the experiments were conducted under the same physical condition and number of replications as in the choice test. Here, however, a single mated naive *D. gelechiidivoris* female (< 24 h post-eclosion) was released into each of four single sleeved Perspex cages (30 x 30 x 30cm), each containing a potted plant with 40 larvae of a specific instar of *T. absoluta* for 24 h. The same procedures and number of dissected larvae were included in the choice test. Cocoons formed in both the choice and no-choice tests were checked twice daily at 09.00 and 18.00 h.

3.2.4 Host instar suitability

The right hind tibia of 20 female wasps each from the four host instars (obtained from 3.2.3) were separated from the point of contact with the thorax under the Leica EZ4D stereomicroscope. The tibiae were placed in 70% ethanol and the lengths measured (x 25), using the Leica EZ4D microscope camera and LAS EZ software 1.5. (LEITZ). The hind tibia length was used as a fitness proxy to assess the effects of host instar on the size of *D. gelechiidivoris* (Roitberg et al., 2001). This proxy was validated by recording the number of eggs in the ovaries of each female (< 24 h post-eclosion) following dissection in a drop of phosphate buffer solution under the Leica EZ4D stereomicroscope.

3.2.5 Potential life-time fecundity

Newly emerged (< 24 h post-eclosion) *D. gelechiidivoris* were obtained from the mother colony and sexed. A pair (male and female) of wasps were placed in a sleeved Perspex cage (6.5 cm x 12 cm x12 cm) and fed with honey as above. Sixty *T. absoluta* first instar larvae on a tomato leaflet, with the petiole plugged into a ball of moistened cotton to delay wilting, were placed in a small glass vial (10 ml). The leaflet was then offered to the parasitoids for 24 h and this procedure was repeated daily until the female died. Male which died prior to female was replaced with a new male (< 24 h post-eclosion). Within 24 h, dead females were dissected, and the remaining mature eggs were counted to assess the residual egg load. Also, dead host larvae were dissected in a drop of phosphate buffer solution, immediately after the exposure time, and the numbers of eggs were recorded. This enabled the estimation of immature mortality (X. Wang pers. comm to P. Aigbedion-Atalor 2018). Female longevity and survival rate, offspring production, offspring sex ratio, and developmental time from egg to adult were determined from the data. The average number of progenies produced per day was estimated based on the total number of progenies produced during each host exposure time interval. Life table fertility parameters such as the gross reproductive rate (*GRR*), net reproductive rate (*R$_0$*), intrinsic rate of natural increase (*r*), mean generation time (*T*), and doubling time (*DT*) were calculated. The *r* was estimated in the same manner as Wang et al. (2018), with the equation: $\Sigma\, e^{-rx}l_x m_x = 1$; in which *x* is the age of the females in d, *l$_x$* is the proportion of individuals surviving at age *x*, and *m$_x$* is the average number of daughters produced per female alive at age *x*. *R$_0$* was calculated by $R_0 = \Sigma\, l_x m_x$. The mean generation time *T* in d is given by $T = \ln R_0/r$. The doubling time in d was estimated as $Dt = \ln(2)/r$. The experiment was replicated 20 times (i.e. 20 females).

3.2.6 Female parasitoid egg maturation dynamics

To determine mature egg load in adult female *D. gelechiidivoris*, 90 wasps were dissected at different age intervals (in days) following emergence in the same physical condition as in section 2.2.1. Newly emerged male and female *D. gelechiidivoris* were collected and placed in cleaned Perspex cages previously provided with food source as in 2.2.1, but without *T. absoluta* larvae. Subsequently, the female parasitoids were collected at seven different time periods (12 hours, 1, 2, 3, 4, 5, and 6 days) post emergence, killed at −20°C, and their ovaries dissected under a stereomicroscope (Leica EZ4D x35). The number of mature eggs per wasp was recorded for each of the seven age groups.

3.2.7 Statistical analysis

Numbers of parasitized hosts and egg load of *D. gelechiidioris* females were tested for normality and homoscedasticity with Shapiro-Wilk's and Bartlett's tests respectively (Bartlett 1937; Shapiro and Wilk 1965). Subsequently, a Generalized Linear Model (GLM), with a negative binomial distribution and log link function was used to assess the differences between parasitized hosts both under choice and no-choice conditions and the egg load of females following eclosion and over time. Data on developmental time and hind tibia length of *D. gelechiidivoris*, reared from different instars of *T. asboluta*, were subjected to two-way Analysis of Variance (ANOVA) to test the effect of larval stage, parasitoid sex and their interaction. Once a significant difference was detected, data was subjected to Tukey's post-hoc test for mean separation. A log-rank test was used to assess the adult survival of *D. gelechiidioris*. All analyses were performed in R. 3.5.1 (R Core Team, 2018).

3.3 Results

3.3.1 Host instar preference and acceptability

Dolichogenidea gelechiidivoris females accepted, and successfully deposited eggs in, all four host larval instars. In the no-choice test, host instar influenced parasitism by *D. gelechiidivoris,* with a higher number of early instars (1st and 2nd), than late instars (3rd and 4th) was parasitized ($\chi^2 = 30.89$, df = 3, $P < 0.001$). This was reflected both in the number of eggs from dissected larvae ($\chi^2 = 16.50$, df = 3, $P < 0.001$) and cocoons formed ($\chi^2 = 19.58$, df = 3, $P < 0.001$) (Fig. 3.1A). Similarly, in the choice test, parasitism rates varied with host instar ($\chi^2 = 114.89$, df = 3, $P < 0.001$), with higher and significantly different percentages of eggs ($\chi^2 = 65.30$, df = 3, P

< 0.001), and cocoons formed ($\chi^2 = 65.30$, df = 3, $P < 0.001$) recorded from the 1st and 2nd instars, respectively (Fig. 3.1B).
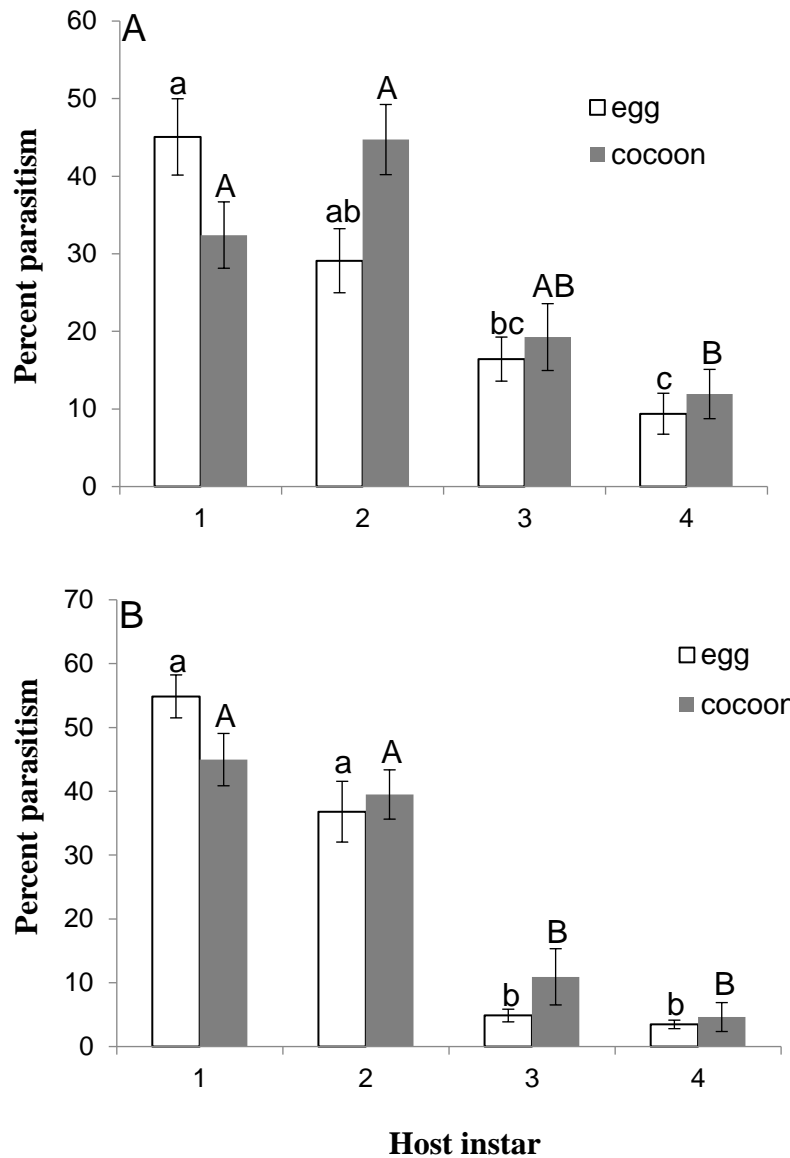
Figure 3.1 Host instar preference and acceptability by *Dolichogenidea gelechiidivoris* in a 24-hour exposure period under (A) no-choice, and (B) choice conditions, as determined both by dissecting larvae following the end of exposure and recording eggs, and by rearing to adult moths or parasitoids. Means ±SE (%) with different letters (small letters) compared the variation of eggs of *Dolichogenidea gelechiidivoris* deposited in the four instar larvae of the host and indicates significantly different (Tukey's HSD, $P < 0.05$). Similarly, means ±SE (as percentage) with different letters (capital letters) compared the variation of *Dolichogenidea gelechiidivoris* cocoon formed from the four instar larvae of *Tuta absoluta* and indicates significantly different (Tukey's HSD, $P < 0.05$).

The sum of cocoons formed ($\chi^2 = 29.19$, df = 3, $P < 0.001$), as well as emerged wasps, reared from each of the four host instars, from the choice and no-choice tests, differed significantly as the 3rd and 4th instars produced significantly fewer wasps as compared to the other instars ($\chi^2 = 37.25$, df = 3, $P < 0.001$) (Table 3.2). However, host instar did not influence the proportion of female wasps produced (Table 3.2).

Table 3.2 Host acceptance and effect of host instar larvae on the development of *Dolichogenidea gelechiidivoris* and progeny sex-ratio (Mean ±SE) under laboratory conditions

Host instar	Number of cocoons (Mean ±SE)	Emerged wasps (Mean ±SE)	Sex ratio (%±SE females)
1	108.00 ± 0.68a	86.00 ± 1.03a	59 ± 1.15a
2	106.50 ± 0.41a	84.00 ± 0.77a	64 ± 1.73a
3	44.50 ± 0.23b	33.50 ± 1.48b	53 ± 1.09a
4	25.00 ± 0.44b	18.00 ± 0.72b	55 ± 1.91a

Means with different lowercase letters were significantly different within columns (Tukey's HSD test, $\alpha = 0.05$).

3.3.2 Host instar suitability

Females of *D. gelechiidivoris* lived 8.51 ± 0.65 d, and host larval stage did not affect their longevity ($F_{1, 152} = 0.33$, $P = 0.802$) (Table 3.3). The size of *D. gelechiidivoris* as estimated by hind tibia length was influenced by host instar. Hind tibia lengths of male and female wasps reared on the first and second instars did not vary significantly but were significantly shorter than those reared on the third and fourth instars ($F_{3, 156} = 52.1$, $P < 0.001$) (Table 3.3). On the other hand, host instar had no influence on the developmental time for either sex ($F_{3, 232} = 0.459$, $P = 0.712$). However, developmental time of female wasps was longer than the male wasps ($F_{1, 232} = 77.497$, $P < 0.001$) (Table 3.3). Egg load of female wasps reared on the different larval instars significantly differed ($\chi^2 = 15.72$, $P = 0.001$), with more eggs recorded in adults from later larval instars (Table 3.3).

Table 3.3 Suitability of host larval instars on some key fitness traits of *Dolichogenidea gelechiidivoris* under laboratory conditions

Host instar	Developmental time from egg to adult (d)		Adult longevity (d)		Hind tibia length (mm)		Egg load (24 h)
	Male	Female	Male	Female	Male	Female	
1	21.13 ± 0.29Aa	24.60 ± 0.49Bb	8.55 ± 0.94Aa	8.75 ± 0.73Aa	0.71 ± 0.01Aa	0.70 ± 0.01Aa	65.55 ± 3.75A
2	20.87 ± 0.23Aa	23.47 ± 0.46Bb	7.95 ± 0.72Aa	8.15 ± 0.69Aa	0.73 ± 0.02Aa	0.71 ± 0.01Aa	75.05 ± 3.20AB
3	20.97 ± 0.25Aa	24.43 ± 0.46Bb	8.50 ± 0.64Aa	8.50 ± 0.65Aa	0.98 ± 0.03Ba	0.99 ± 0.03Ba	84.10 ± 3.34B
4	21.17 ± 0.40Aa	23.53 ± 0.48Bb	7.60 ± 0.70Aa	8.65 ± 0.54Aa	0.94 ± 0.05Ba	0.98 ± 0.04Ba	81.08 ± 4.05B

Means with the same uppercase letters indicate significantly different within columns (Tukey's HSD test, $\alpha = 0.05$). Within rows, means with different lowercase letters were significantly different (Tukey's HSD test, $\alpha = 0.05$).

3.3.3 Potential lifetime fecundity and demographical indexes

Females of *D. gelechidivoris* produced 103 ± 8 eggs on average. Females began oviposition following eclosion (< 24 h old) with the highest number of offspring produced within the first three days, and thereafter, demonstrating a significantly steady decline in offspring production with age (χ^2 = 142. 99, *P* < 0.001) (Fig. 3.2A). Similarly, maternal age influenced the percentage of female offspring production (χ^2 = 156. 76, *P* < 0.001), in that no female was produced after 13 d (Fig. 3.2B), corresponding to the significantly lower offspring production (Fig. 3.2A). As expected, the age of females also affected their survival (Fig. 3.3). Residual egg load recorded in the ovaries of dead females was 25 ± 6. The estimation of the demographic parameters showed the gross and net reproductive rates as 72 and 39 daughters per female, respectively, while the mean generation time was 20 d. The intrinsic rate of natural increase was 0.18.
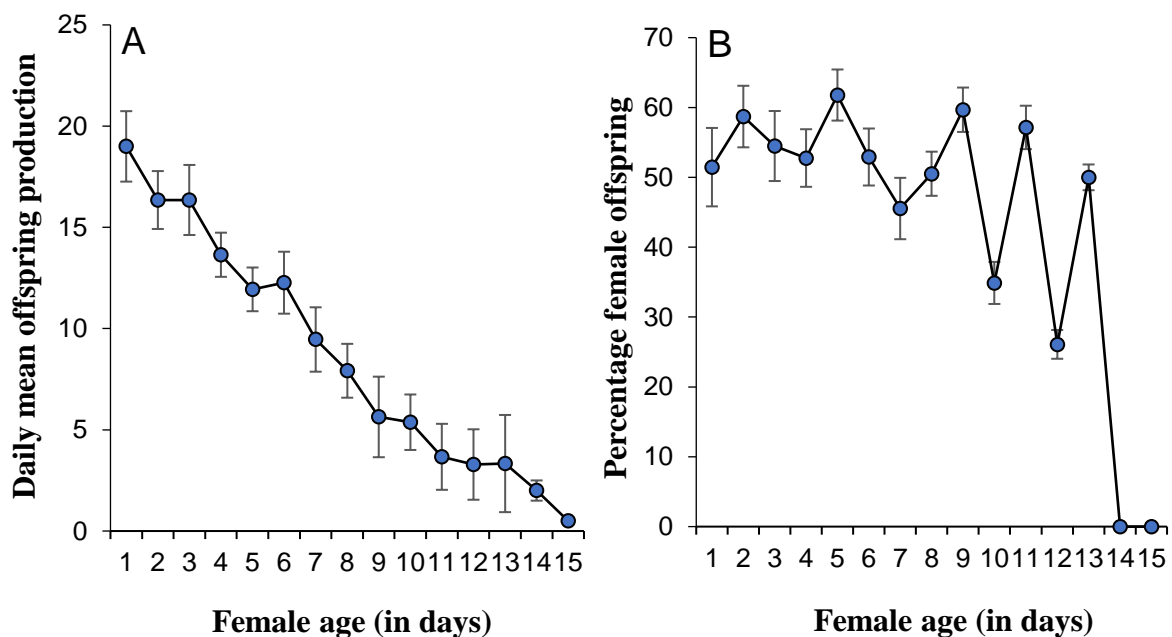
Figure 3.2 *Dolichogenidea gelechiidivoris* (A) lifetime reproduction and, (B) offspring sex when parasitizing *Tuta absoluta*. Values (means ± SEM) are number of progeny produced daily and percentage of female offspring (n =20 females).
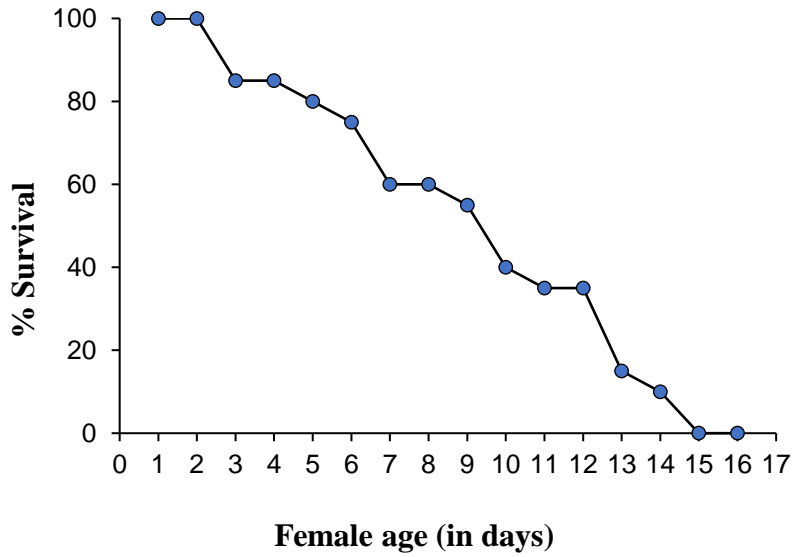
Figure 3.3 Survival curve of adult females of *Dolichogenidea gelechiidivoris* (n =20 females).

3.3.4 Female parasitoid egg maturation dynamics

Egg load of *D. gelechiidivoris* differed significantly over time ($\chi^2 = 46.74$, $P < 0.001$), with females emerged with 74 ± 4.0 mature eggs, and reaching a maximum of ~ 118 at 2 d old (Fig. 3.4). Mature egg load, however, did not differ significantly after the third day (Fig. 3.4).
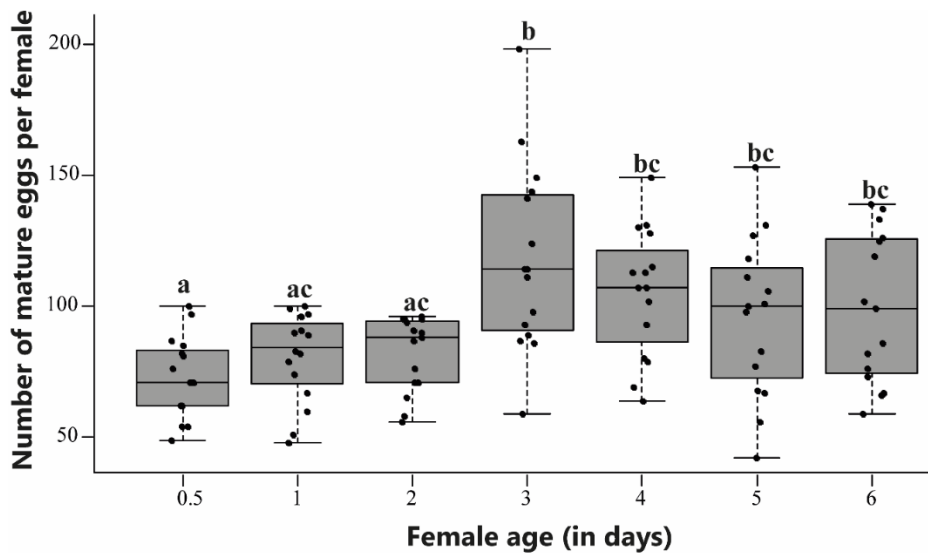
Figure 3.4 Egg maturation dynamics of host-deprived, but honey-fed, *Dolichogenidea gelechiidivoris* females. Boxplot whiskers indicate ±1.5 interquartile range limits of the data. Boxplots with different letters depict significant differences as grouped by a generalized linear model and followed by Tukey's HSD test ($P < 0.05$, n= 15).

3.4 Discussion

In this first pre-release evaluation study of *D. gelechiidivoris*, its efficacy in attacking, and successfully parasitizing all four larval instar stages of *T. absoluta*, albeit preferentially choosing the early instars for oviposition both under choice and no-choice situations was recorded. This finding was not unexpected because evolutionarily, individuals of the braconid parasitoid wasp belonging to the subfamily Microgastrinae oviposit into early instars of their host species (Whitefield et al., 2018, and references therein). However, whether this evolutionary oviposition adaptation corresponds to, or reflects progeny reproductive fitness returns remains largely unknown. That said, the reproductive success of female parasitoids, notably, koinobiont parasitoids, are solely dependent on their ability to accurately assess the suitability of a host for larval development (Vinson and Iwantsch, 1980). This means that deposition of eggs in maladaptive hosts would beleaguer the fate of the parasitoid's progeny (Harvey and Strand, 2002; Henter and Via, 1995; Kraaijeveld et al., 2002; Vinson and Iwantsch, 1980). However, this is not the case for *D. gelechiidivoris* with *T. absoluta* as a host, as all four instar larvae of the host are suitable. Although significantly fewer wasps emerged from the late instar larvae (3rd and 4th) of *T. absoluta*, resultant of both the significantly lesser searching time spent by females and the fewer cocoons formed thereof, all four host instars supported the juvenile stage development of *D. gelechidiivoris*. All four host instars also produced viable progeny of the parasitoid with high female proportions.

Females of *D. gelechiidivoris* emerged with a high mature egg load which increased significantly after the second day but remained quite similar thereafter. Ellers et al. (2000) and Jervis et al. (2001) showed that rather than egg maturation, the total offspring produced by a parasitoid is dependent on the adult longevity, mature egg load, number of hosts encountered, and oviposition dynamics. Our results agree with the conclusions of both studies. In this context, the daily offspring production of *D. gelechiidivoris* was significantly higher in the first three days of emergence, coinciding with the high egg load at emergence, but thereafter declined with the age despite the increase in egg load over time. Evidently, the efficacy and foraging of parasitoids are not disassociated from ovarian dynamics as the physiological status of the ovaries may determine crucial aspects of its reproductive behaviour such as oviposition rate (Jervis et al., 2001; Wang et al., 2018). Strictly pro-ovigenic (full lifetime complements of mature eggs at emergence) (Flanders, 1950) parasitoids are rare (Jervis et al., 2001). Except *Cotesia flavipes* (Cameron) (Hymenoptera: Braconidae) (Potting et al., 1997), none of the 76

braconid species studied by Jervis et al. (2001) were strictly pro-ovigenic. Results of the egg maturation dynamics of *D. gelechiidivoris* indicate that it is a weakly synovigenic species, as the majority of its lifetime egg load were mature upon emergence albeit with a significant increase over time. The continuum from strongly to weakly synovigeny has been previously documented (e.g., Jervis and Copland, 1996; Jervis et al., 2001; Quicke, 1997). The concentration towards the production of mature oocytes early in the adult life of parasitoids are associated with trade-offs (Jervis et al., 2001). Ellers and Van Alphen (1997) and Ellers et al. (1998) recorded that lifespan among strains of the parasitoid wasp *Asobara tabida* Nees (Braconidae: Alysiinae) was inversely related to oocytes' maturity at emergence. This finding is indeed validated by the theory of life-history, predicting that lifespan is traded-off as a result of the intensification of reproductive effort towards early adult life (Jervis et al., 2001). Here, the production of mature oocytes early in the adult life of *D. gelechiidvoris* appears to affect its longevity. This is typical of proovigenic and weakly synovigenic parasitoids (Jervis et al., 2001).

Life table parameters such as net reproductive rate and the intrinsic rate of natural increase can be used in estimating a parasitoid's potential population growth and fitness on a host species (Birch, 1948; Gaston, 1988; Wang et al., 2018). The net reproductive rate R_o is a crucial parameter which indicates the growth rate of a population from a generation to the next one (Birch, 1948). In this study, the R_o of 39 daughters per female was obtained. This was mainly attributed to the low mortality rates of immature stages of *D. gelechiidivoris*, thus indicating a high suitability of *T. absoluta* as host for this parasitoid at least under laboratory conditions. Using the rearing method documented in this study, the mean generation time obtained showed that *D. gelechiidivoris* needs only 20 d to complete one generation on *T. absoluta*. Thus, the parasitoid can have several generations on its host within a single tomato growing season, which makes it a potential biological control candidate of *T. absoluta*. Under field conditions R_o will of course be reduced by environmental stochasticity that kill parasitized host larvae (e.g. predators and hyperparasitoids) and adult parasitoids (extreme conditions such as temperature) not present in the laboratory.

Overall, our results agree with reports from South America. For example, Redolfi and Vargas (1983), reported the duration of the immature stage (egg, larva, and pupa) of *D. gelechiidivoris* was 22 d at 25 °C. A duration of 21 d at 26 ± 4°C (range: 24 to 29°C) with male wasps

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developing significantly faster than female wasps was recorded in this study. Similar to our findings on the parasitoid's host instar oviposition preference, Redolfi and Vargas (1983) reported that *D. gelechiidivoris* demonstrates a preference for oviposition in early host instars. Bajonero et al. (2008) showed temperature effects on the life-history traits of *D. gelechiidivoris*. The average longevity of adult *D. gelechiidivoris* reported by the latter authors was 8.6, 6.9, 5.4, and 1.8 d at 14 °C, 20 °C, 26 °C, and 32 °C, respectively. Here, although temperature effects on *D. gelechiidivoris* were not investigated, an average adult longevity of 8.5 d at an average of 26 ± 4 °C was recorded. Of significant importance, Bajonero et al. (2008) demonstrated that the suitable temperature regimes for rearing *D. gelechiidivoris* lie between 20 °C and 26 °C and further suggested 20 °C as the optimum temperature for the immature development of the parasitoid. This suggests that *D. gelechiidivoris* may be maladapted to areas of Africa with average temperature exceeding 30 °C; herein the longevity of the parasitoid is 1.8 d (see. Bajonero et al., 2008). Nevertheless, *T. absoluta* is also constrained by temperature. At 30 °C, the pest demonstrates a high reproductive performance and longevity but both life-history parameters decline significantly with increasing temperature above 30 °C (Martins et al., 2016). *Dolichogenidea gelechiidivoris* can parasitize *T. absoluta* over a wide range of temperatures, including 32 °C (Bajonero et al., 2008) which is within the range of tomato production in Africa (Saidi et al., 2013). The parasitoid has been recorded across a wide range of altitudes having been recorded at 1000 masl (Mujica and Kroschel, 2013; Mujica pers. comm to Aigbedion-Atalor 2018), and at 3550 masl in Huasahuasi, and 3850 masl in the Rio Mantaro valley in the central Peruvian highlands (Kroschel and Cañedo, 2009). Reports of its occurrence in both high and low altitudinal areas have been documented in the coastal regions of Chile, Colombia, and Peru; including the Andean highland (e.g., Agudelo and Kaimowitz, 1997; Palacios and Cisneros, 1995; Rojas, 1997; Valencia and Penaloza, 1990; Vallejo, 1999; Wanumen, 2012).

The information reported in this study is crucial for subsequent studies, especially mass rearing for field releases. If approved for release in Kenya and across Africa, non-target effects of *D. gelechiidivoris* is not anticipated due to its high parasitism rate on *T. absoluta*. Nonetheless, there is need for further assessments of *D. gelechiidivoris* including host specificity testing and its interactions with the zoophytophagous predator, *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae), which is widespread in Kenya (E. Deletre, Personal communication 2018), and the indigenous *Trichogramma* spp. that have been mass-released in North Africa (Cherif et al.,

2019b; El-Arnaouty et al., 2014; Kortam et al., 2014; Mansour and Biondi, 2020; Rizk, 2016; Zouba et al., 2013b). Subsequently, combined mass-releases of the parasitoids *Trichogramma* spp and *D. gelechidivoris*, as well as periodic augmentative releases of both species, should be made. This approach could be crucial for the overall reduction of the infestation level and socio-economic impacts of *T. absoluta* in Africa.

CHAPTER 4

Behavioural interactions between *Dolichogenidea gelechiidivoris* and the zoophytophagous bug *Nesidiocoris tenuis*: implications for biological control of *Tuta absoluta* in Africa

4.1 Introduction

In the early era of biological control, the rationale for the use of multiple natural enemies was justified by the likelihood of increasing cumulative efficacy – the so-called "lottery approach" (Myers, 1985). Although some notable successes were recorded (Denoth et al., 2002; Keller, 1984; Myers, 1989), because interactions between two or more natural enemies are not straightforward, the outcome may be counterproductive (Rosenheim et al., 1995; Snyder and Ives, 2001). Interactions could be synergistic – i.e. the cumulative efficacy of both species being significantly higher than that of the two natural enemies alone, or additive – when both natural enemies are more effective than the most effective species alone but less effective than the added efficacy by each species alone (Turner et al., 2010). In other cases, interactions may be equivalent – i.e. when the combined impacts of both natural enemies are equivalent to the more effective of the two species as depicted by the cotton aphid parasitoid, *Lysiphlebus testaceipes* (Cresson) (Hymenoptera: Braconidae), and the convergent lady beetle *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae) (Brodeur and Rosenheim, 2000; Colfer and Rosenheim, 2001), or inhibitory – when both natural enemies cause significantly less effectiveness than that induced by the most effective species alone (Bilu and Coll, 2007; Turner et al., 2010). More extreme adverse effects include the possibility of competitive exclusion (Ehler and Hall, 1982; Keller, 1984; Myers, 1985), such as the case of *Aphidius colemani* Viereck (Hymenoptera: Aphidiidae) by its intraguild predator *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) (Bilu and Coll, 2007). These different possible outcomes indicate that concurrent augmentation of multiple natural enemies for the control of a host pest species does not necessarily equate to success and may not be more effective than either agent alone; especially when a more effective natural enemy is displaced by a less effective but competitively superior one (Denoth et al., 2002) or when subjected to intraguild interactions (IGIs) – competition between high-trophic-level consumers that share the same prey or host (Gagnon et al., 2011; Staudacher et al., 2016). Intraguild predation (IGP), consists of the predatory behaviour of one natural enemy species (intraguild predator) on another (intraguild prey) (Naselli et al., 2017), and it is the most researched IGIs type. IGP

could be direct or indirect such as consumption of parasitized hosts or reduction in oviposition performance by a parasitoid species due to the presence of its intra-guild predator (Gagnon et al., 2011; Rosenheim et al., 1995). In virtually almost all cases, the occurrence of intraguild predation between predators and parasitoids are linked to the inability of generalist predators to discriminate between parasitised and unparasitised prey (Chailleux et al., 2013; Gkounti et al., 2014; Rosenheim et al., 1995).

Modern approach to biological control highlights the need for proper evaluations justifying the use of multiple agents (Denoth et al., 2002; Pederson and Mills, 2004). Indeed, this approach can significantly reduce unnecessary releases of agents and increase synergism or additive effects because when properly utilized, multiple agents can significantly increase the mortality of a target pest (Stiling and Cornelissen, 2005). Studies on IGP with *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) natural enemies have been so far conducted with egg parasitoids and mirids and with larval ectoparasitoids and mirids (e.g., Chailleux et al., 2017; Naselli et al. 2017), but never with endoparasitoids. This chapter, therefore, presents a novel insight into this lacuna by disentangling the nature of interactions between a predatory bug *Nesidiocoris tenuis* (Reuter) (Hemiptera: Gelechiidae) and the specialist endoparasitoid *Dolichogenidea gelechiidivoris* Marsh (Hymenoptera: Braconidae) with *T. absoluta* as host. Because *N. tenuis* can prey on early host larval instars (1st and 2nd) of *T. absoluta* (Urbaneja et al., 2009) – the preferred oviposition host stage of *D. gelechiidivoris* (Chapter 3) – the aim of this chapter was to investigate the direct interactions between the omnivore and the parasitoid. We hypothesized that without *T. absoluta* eggs (the preferred host stage of the predator), *N. tenuis* would inflict intraguild predation on the immature stages (egg, larva, and cocoon) of *D. gelechiidivoris* within parasitized host larvae thereby reducing the progeny of the parasitoid. The outcomes of the interactions between these two natural enemies are discussed both from an ecological perspective and in the context of biological control of *T. absoluta*.

4.2 Materials and Methods

4.2.1 Insect rearing

Colonies of *T. absoluta*, *D. gelechiidivoris* and *N. tenuis* were reared and maintained in a quarantine facility of the International Centre of Insect Physiology and Ecology (*icipe*), Nairobi, Kenya (1°17'8.844"S36°49'12.108"E). Here, two hundred cocoons of *D. gelechiidivoris* were received from the International Potato Centre (CIP) in Peru

(16°57'36.252"N96°28'32.052"W) and placed in a single sleeved PERSPEX® glass cage (30 × 30 × 30 cm). This was used to establish the parasitoid's colony. *Tuta absoluta* (eggs, larvae, and pupae) and *N. tenuis* (adults) were collected from infested tomato plants in 10 counties of Kenya (Table 4.1). The infested tomato plants (with *T. absoluta* and *N. tenuis*) were placed in a single sleeved PERSPEX® glass cages (65 × 45 × 45 cm). Following eclosion, adults of *T. absoluta* were aspirated into new sets of single sleeved PERSPEX® glass cages (65 × 45 × 45 cm) each containing four potted tomato plants (cv. Moneymaker) for oviposition. *Nesidiocoris tenuis* adults were placed in similar cages containing four potted tomato plants. Subsequently, adults of *D. gelechiidivoris* were placed in cages containing *T. absoluta* larvae for host parasitization. Food sources (streaks of 80% honey solution) were smeared on the top sides of the cage. In addition to the honey solution, non-viable eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidea) and commercial pollen (M. LACARTE, 86800 Terce) were offered to *N. tenuis*. The environmental conditions in the quarantine facility were maintained at 25 ± 1°C, 65 ± 5% RH, and photoperiod of 12:12 L:D.

Table 4.1 Counties of Kenya where *Tuta absoluta* was collected to maintain the genomic pool of the established laboratory colony

County	GPS coordinates	Number of sites sampled
Kajiado	1° 50' 30.984" S 36° 47' 21.3648" E	14
Kwale	4° 10' 31.116" S 39° 27' 11.952" E	7
Limuru	1° 6' 33.66" S 36° 38' 35.592" E	11
Machakos	1° 31' 6.348" S 37° 16' 0.8364" E	13
Meru	0° 2' 47.004" N 37° 39' 9.8928" E	8
Nakuru	0° 16' 53.364" S 36° 4' 42.3084" E	15
Nyeri	0° 25' 16.14" S 36° 56' 57.8724" E	2
Siaya	0° 3' 44.568" N 34° 17' 20.616" E	1
Taita Taveta	3° 23' 31.92" S 37° 40' 26.832" E	12
Mwea	1° 41' 47.04" S 37° 25' 2.712" E	5

4.2.2 Intraguild predation by Nesidiocoris tenuis on Dolichogenidea gelechiidivoris

Under the same environmental conditions above, nine treatments and three controls were used to assess the intraguild interaction between *N. tenuis* and *D. gelechiidivoris* on the larvae of *T. absoluta* (Table 4.2). For each treatment, a tomato leaflet (cv. Moneymaker) with 20 first instar larvae of *T. absoluta* and the petiole inserted in a moistened cotton wool ball to prevent early

wilting, was placed in a small single sleeved PERSPEX® glass cage (6.5 cm x 12 cm x12 cm) in which little streaks of 80% honey solution were smeared. The treatments (Table 4.2) included (T1): introduction of four *N. tenuis* before a female *D. gelechiidivoris* – here, four naïve *N. tenuis* (2 to 5 day-old) were placed in a PERSPEX® cage (6.5 cm x 12 cm x12 cm), housing a tomato leaflet with 20 first instar larvae of *T. absoluta*, for 48 hours. Following the removal of *N. tenuis*, a naïve mated female *D. gelechiidivoris* (1 day-old) was then placed in the cage and removed after 24 hours. The leaflet was retained in the cage for subsequent development of the larvae albeit with an intermittent re-supply of diet (tomato leaves). The same number of larvae, leaflet, experimental arena, exposure time (48 h for *N. tenuis* and 24 h for *D. gelechiidivoris*), and biological characteristics of both natural enemies described above were used for the other eight treatments (T2): two *N. tenuis* prior to a female *D. gelechiidivoris*, (T3): One *N. tenuis* prior to a female *D. gelechiidivoris*, (T4): a female *D. gelechiidivoris* prior to four *N. tenuis*, (T5): a female *D. gelechiidivoris* prior to two *N. tenuis*, (T6): a female *D. gelechiidivoris* prior to one *N. tenuis*, (T7): simultaneous introduction of four *N. tenuis* and a female *D. gelechiidivoris*, (T8) simultaneous introduction of two *N. tenuis* and a female *D. gelechiidivoris*, (T9) simultaneous introduction of one *N. tenuis* and a female *D. gelechiidivoris*. A control, (C): one female *D. gelechiidivoris* alone, was included in the experiment. Also, two additional controls (LC1): four *N. tenuis* only, and (LC2): a tomato leaflet with 20 first instar larvae of *T. absoluta* without the natural enemies were included to serve as controls only for *T. absoluta* larvae mortality (see Table 4.2 for further details). In all treatments and controls, the number of dead *T. absoluta* larvae was counted and recorded 7 days after the start of the experiments. Six replicates were carried out per treatment. All experiments were carried out at (25 ± 1°C, 65 ± 5% RH, and photoperiod of 12:12 L:D).

Table 4.2 Treatments structure used in assessing the interaction between *Dolichogenidea gelechiidivoris* and *Nesidiocoris tenuis* on the larvae of *Tuta absoluta*

Treatment	Delineation	No. of Nt	No. of Dg	Replicates
(T1) Nt4Dg	Four *N. tenuis* introduced for 48 h before a female *D. gelechiidivoris*	4	1	6
(T2) Nt2Dg	Two *N. tenuis* introduced for 48 h before a female *D. gelechiidivoris* for 24 h	2	1	6
(T3) Nt1Dg	One *N. tenuis* introduced for 48 h before a female *D. gelechiidivoris*	1	1	6
(T4) DgNt4	A female *D. gelechiidivoris* introduced for 24 h before four *N. tenuis*	4	1	6
(T5) DgNt2	A female *D. gelechiidivoris* introduced for 24 h before two *N. tenuis*	2	1	6
(T6) DgNt1	A female *D. gelechiidivoris* introduced for 24 h before one *N. tenuis*	1	1	6
(T7) Dg+Nt4	Simultaneous introduction of both natural enemies (Nt: 48 h and Dg: 24 h)	4	1	6
(T8) Dg+Nt2	Simultaneous introduction of both natural enemies (Nt: 48 h and Dg: 24 h)	2	1	6
(T9) Dg+Nt1	Simultaneous introduction of both natural enemies (Nt: 48 h and Dg: 24 h)	1	1	6
(C) Dg	*Dolichogenidea gelechiidivoris* alone for 24 h	0	1	6
(LC1) Nt4	Four *N. tenuis* alone for 48 h	4	0	6
(LC2) Control	No natural enemy present	0	0	6

The predator was allocated more exposure time (48 h) than the parasitoid (24 h) with the intention of maximizing predation, that is, increasing the likelihood of predation. Nt indicates *Nesidiocoris tenuis*, while Dg indicates *Dolichogenidea gelechiidivoris*. Both natural enemies were host and food deprived prior to the start of the experiments. Numerals appended to "Nt" indicate the number of *N. tenuis* used for each assay. For example, Nt4 indicates that four *N. tenuis* were used in the experiment. Note that LC1 and LC2 served as controls only for *Tuta absoluta* larval mortality and were not included for assessing the effect of the predator on the parasitoid.

4.2.3 Efficacy of Dolichogenidea gelechiidivoris with and without Nesidiocoris tenuis on Tuta absoluta

Under the same conditions described above, the effectiveness of *D. gelechiidivoris* and *N. tenuis* (both alone and in combination) in decreasing population density of *T. absoluta* was

evaluated. Here, tomato plants were exposed to *T. absoluta* for egg-laying in single sleeved PERSPEX® glass cages (65 × 45 × 45 cm) for 24 hours. Thereafter, 60 eggs were retained on two opposite leaflets of the plant, while excessive eggs were removed using a camel hairbrush and other plant leaflets cut off. The leaflets bearing the eggs were carefully inserted in a plastic nalophan bag (used as test arena) and the proximal end of each bag was attached to the plant stem. The following treatments (i.e. biocontrol agents) were introduced into each bag for 24 hours (Nt2): two *N. tenuis* alone, (Dg2): two *D. gelechiidivoris* alone – here, eggs had developed into 1st instar larvae before the parasitoids were introduced, (Nt2Dg2): two *N. tenuis* and two *D. gelechiidivoris* – here, the eggs remaining after *N. tenuis* feeding were retained until larvae formation prior to the introduction of the parasitoids, (C): control (i.e. none of the two natural enemies present). After being exposed to the natural enemies, the infested leaflets were detached from the plant stem and the petioles inserted in moistened cotton wool ball to prevent early wilting. Subsequently, the leaflets were placed in small PERSPEX® glass cages (6.5 cm x 12 cm x12 cm) for subsequent development of the larvae albeit with an intermittent re-supply of diet (fresh tomato leaves). The cages with the leaflets were kept in an insect growth chamber with a constant environmental condition of 25 ± 1°C, 65 ± 5% RH, and photoperiod of 12:12 L:D. Daily checks were made, and the number of emerging moths, cocoons and adult parasitoids recorded. Each experiment was replicated six times.

4.2.4 Statistical Analyses

All analyses were performed in R. 4.0.0 (R Core Team, 2020) and the R Studio graphical user interface (version 1.2.5042). Owing to the binary nature of the data from *T. absoluta* mortality (Dead vs Alive), we used the generalised linear model (GLM) with binomial distribution and log link function to test whether this variable was influenced by the different predator densities. We established the significance of the model using analysis of deviance (with Chi-square test). Data from the number of *D. gelechiidivoris* cocoons formed and emerged adults, and the number of females from each treatment were normally distributed (Shapiro-Wilks tests: $P >0.05$) and their variance was homogenous (Bartlett's test: $P>0.05$). Therefore, we ran the analysis of variance (ANOVA). Data on the efficacy of *D. gelechiidivoris* and *N. tenuis* both alone and in combination on the population density of *T. absoluta* followed a normal distribution model and their variance was similar. So, we performed the ANOVA followed by the Student-Newman-Keuls (SNK) post-hoc tests to separate the means. All statistical significances were detected at $P<0.05$.

4.3 Results

4.3.1 Intraguild predation by Nesidiocoris tenuis on Dolichogenidea gelechiidivoris

Host larvae feeding of *N. tenuis* did not affect the oviposition performance of *D. gelechiidivoris* and its corresponding number of progenies. With or without *D. gelechiidivoris*, *N. tenuis* host larvae feeding was generally low and not significant (GLM, $\chi^2 = 70.852$, df = 11, $P = 0.910$) (Fig. 4.1).
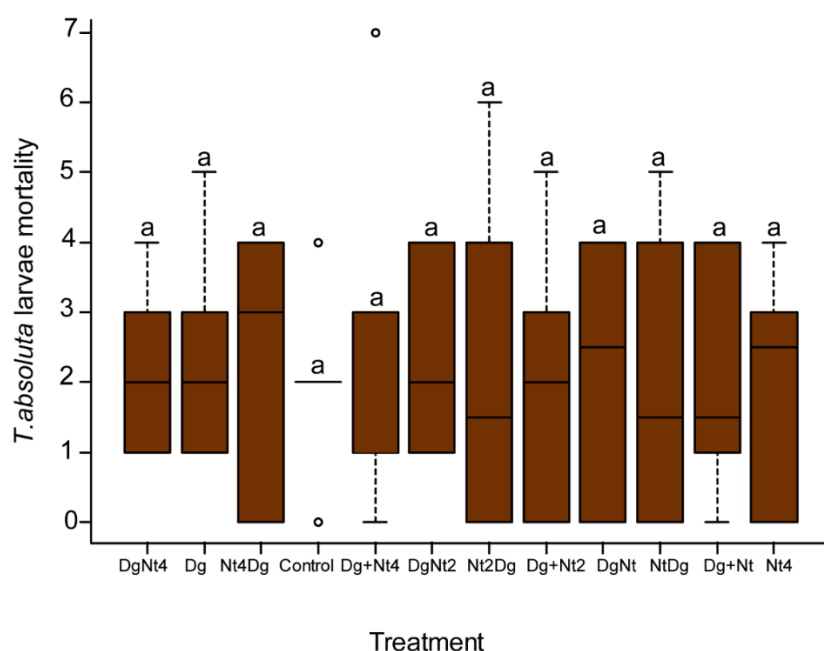
Figure 4.1 *Tuta absoluta* larvae mortality seven days following the start of the experiment in the different treatments after allocating a preceding 48-hour host predation exposure time to *Nesidiocoris tenuis* in varying density combinations (1, 2, and 4) and sequence of introduction with a female *Dolichogenidea gelechiidivoris*.

Nesidiocoris tenuis did not demonstrate a preference for parasitized host larvae. This was reflected in the number of *D. gelechiidivoris* cocoons formed ($F_{9,50} = 0.59$, $P = 0.861$) (Fig. 4.2), as well as in the number of adult parasitoids which emerged from the different treatments ($F_{9,50} = 0.41$, $P < 0.92$) (Fig. 4.3). Similarly, no significant differences were recorded in the number of *D. gelechiidivoris* females that emerged in each of the treatments ($F_{9,50} = 0.32$), $P = 0.966$) (Fig. 4.4).

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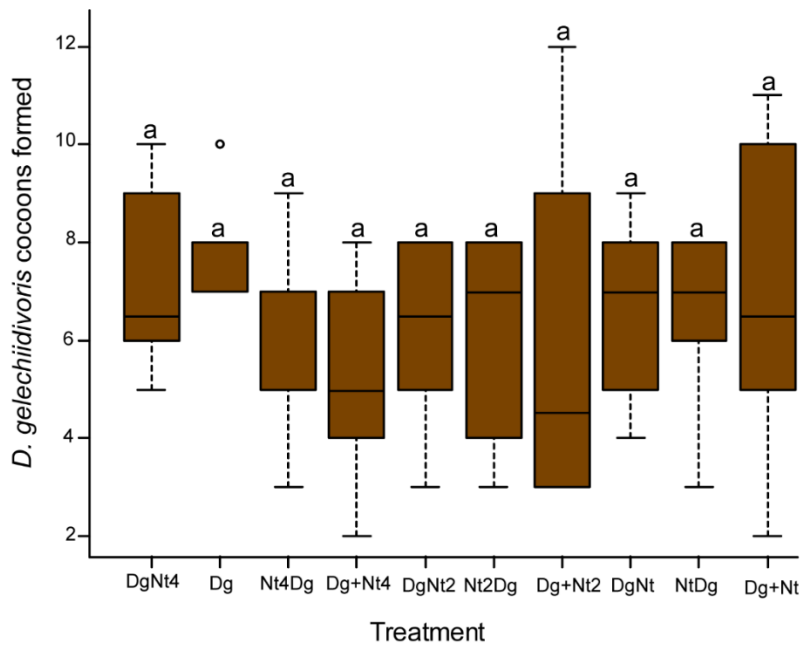
Figure 4.2 Number of *Dolichogenidea gelechiidivoris* cocoons formed in each of the different treatments following a 48-hour host predation exposure time to *Nesidiocoris tenuis* in varying density combinations (1, 2, and 4) and sequence of introduction with a female *D. gelechiidivoris*.
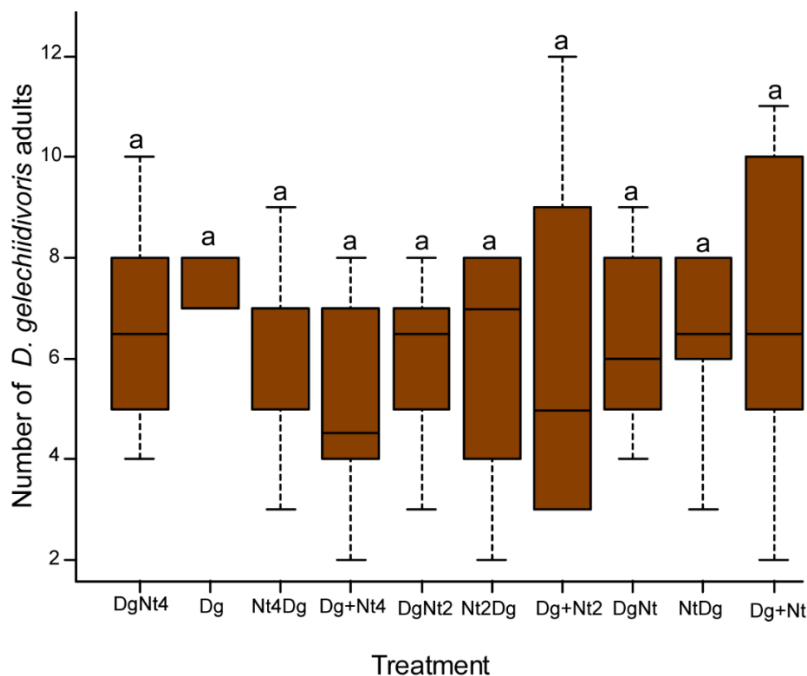
Figure 4.3 Number of *Dolichogenidea gelechiidivoris* adult eclosion in each of the different treatments following a 48-hour host predation exposure time to *Nesidiocoris tenuis* in varying

density combinations (1, 2, and 4) and sequence of introduction with a female *D. gelechiidivoris.*
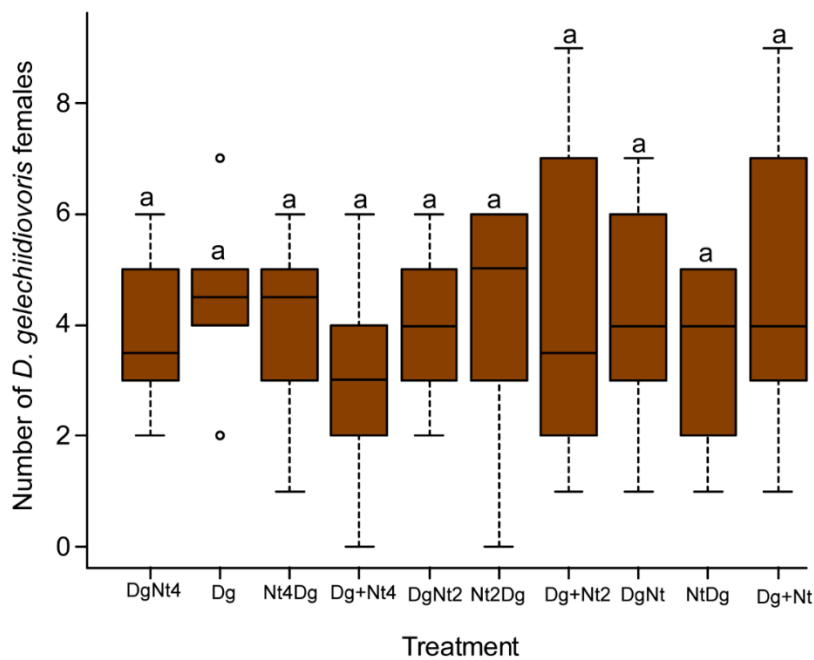
Figure 4.4 Number of female *Dolichogenidea gelechiidivoris* from each of the different treatments.

4.3.2 Efficacy of Dolichogenidea gelechiidivoris with and without Nesidiocoris tenuis on Tuta absoluta

Dolichogenidea gelechiidivoris, *N. tenuis*, and the combination of both natural enemies significantly reduced the number of *T. absoluta* adult eclosions respectively ($F_{3,20} = 56.51$ $P <$ 0.001). Although both natural enemies had a similar efficacy on the host (Fig. 4.5), their combined efficacy was significant as *T. absoluta* adult eclosion was significantly more reduced when both biocontrol agents were combined than when they occurred alone (Fig. 4.5).
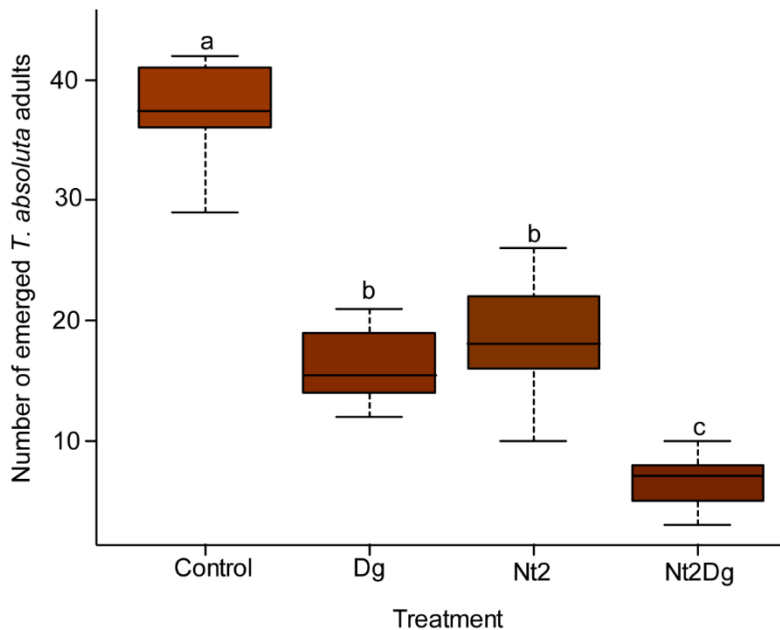
Figure 4.5 Number of *Tuta absoluta* adult emergence. Boxes with different lowercase letters, following ANOVA, depict significantly different (SNK test *P* < 0.05).

4.4 Discussion

Regardless of *N. tenuis* density and the sequence in which it was combined with *D gelechiidivoris*, *N. tenuis* did not affect the oviposition performance of *D. gelechiidivoris* nor the number of the parasitoid's adult progeny. This was largely due to the little or no host larval feeding by *N. tenuis*. Also, there was no evidence that *N. tenuis* attacked *D. gelechiidivoris* females or affected the oviposition performance thereof. These findings thus fail to accept our hypothesis of inhibitory interaction between both natural enemies and suggest that *N. tenuis* does not inflict intraguild predation on *D. gelechiidivoris*. Although both *N. tenuis* and *D. gelechiidivoris* effectively reduced the population density of *T. absoluta*, the combination of both natural enemies, however, proved more effective than either agent alone, indicating a possible synergistic interaction between both agents. This study, therefore, highlights the potential of using *D. gelechiidivoris* and *N. tenuis* for biological control of *T. absoluta* in Africa. Similar synergistic effects between specialist parasitoids and generalist omnivorous predators of *T. absoluta* have been reported. For example, Chailleux et al. (2017) documented that the combination of the predator *Macrolophus pymaeus* Wagner (Hemiptera: Miridae) and the idiobiont parasitoid *Stenomesius japonicus (*Ashmead) (Hymenoptera: Eulophidae), showed complementary functional traits which resulted in a higher control of *T. absoluta* than when either natural enemy occurred alone. In another related study, Chailleux et al. (2013) reported on the combined effects of *M. pymaeus* and Trichogramma egg parasitoids. Although

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intraguild predation by *M. pygmaeus* was inflicted on *Trichogramma achaeae* Nagaraja and Nagarkatti, the risk of the intraguild predation was dependent on the larval developmental stages of *T. achaeae* in *T. absoluta* eggs and the combination of both natural enemies was shown to be more effective for the control of *T. absoluta* when compared to the efficacy of the predator alone, thus suggesting an additive interaction between both natural enemies (Chailleux et al., 2013).

Indeed, the use of two or more natural enemies for pest control when synergism or additive interaction occur is recommended because such interactions usually increase the overall mortality of the target pest (Chailleux et al., 2013; Denoth et al., 2002; Stiling and Cornelissen, 2005). It is prudent to acknowledge that egg parasitoids are more susceptible to intraguild predation by generalist egg predators such as *M. pygmaeus* and *N. tenuis* than larval parasitoids (Calvo et al., 2012; Chailleux et al., 2013; 2017). In this context, therefore, the results of this study support the integration of *D. gelechiidivoris* with generalist egg predators such as *N. tenuis* and *M. pygmaeus* could potentially improve the overall efficacy of biological control of *T. absoluta* in Africa.

Several indigenous natural enemies such as *Bracon nigricans* Szépligeti (Hymenoptera: Braconidae), *Bracon* sp. (Hymenoptera: Braconidae), *Dolichogenidea appellater* (Telenga) (Hymenoptera: Braconidae), *Trichogramma bourarachae* Pintureau and Babault (Hymenoptera: Trichogrammatidae), *M. pygmaeus*, *Necremnus tutae* Ribes and Bernardo (Hymenoptera: Eulophidae), *Trichogramma cacoeciae* (Marchal) (Hymenoptera: Trichogrammatidae), and *Rhynocoris segmentarius* (Germar) (Hemiptera: Reduvidae) (Cherif et al., 2019b; Idriss et al., 2018; Mansour and Biondi, 2020; Zouba et al., 2013a; 2013b) have been reported as effective for the biological control of *T. absoluta* in Africa. However, few studies evaluating the interactions between some of these natural enemies in Africa have been carried out (Mansour et al., 2018). It is therefore important that further studies should investigate the interactions and possible combinations of *D. gelechiidivoris* and the aforementioned occurring natural enemies in Africa where the socio-economic impacts of *T. absoluta* are devastating.

In conclusion, augmentative releases of *N. tenuis* and *D. gelechiidivoris* can effectively reduce the infestation levels of *T. absoluta* because in the natural ecological scenario of a tomato

agroecology, all host life stage of the pest usually occur, albeit in varying densities, thus indicating that the preferred host life-stage each of the natural enemies would always be present, thereby limiting the outcome of predation on *D. gelechiidivoris*-parasitized *T. absoluta* larvae. Differences in the exploitation of oviposition and feeding resources have been theoretically and experimentally shown to promote coexistence between species of biocontrol agents (Brown et al., 1997; Wilson et al., 1999). In this natural scenerio, *N. tenuis* will preferentially feed on, and reduce densities of *T. absoluta* eggs, while *D. gelechiidivoris* will reduce the larvae stage of the pest, consequently reducing the overall infestation level of the pest and alleviating its burden on tomato growers in Africa.

CHAPTER 5

GENERAL DISCUSSION

5.1 Introduction

In Africa, agriculture which mainly consists of land cultivation for growing food and cash crops, animal rearing, forestry, and hunting is the driver of sustainable livelihoods (FAO, 2019). The majority of people (about 61.4%) in sub-Saharan Africa live in rural households and about 57.3 % of people are engaged in agricultural-related means of livelihood (Dercon and Gollin, 2014). This indicates that agriculture is a key diver of the African economy (Dercon and Gollin, 2014). Therefore, it is crucial to facilitate the growth of this sector by providing and implementing policies which ensure that the factors that can limit production and induce livelihood losses such as, land availability, phytosanitary and quarantine measures, pests and diseases, and access to funding especially to smallholder farmers, are rapidly and adequately addressed (Zimmermann et al., 2009). Three syntheses provide justifications for polices which favours agricultural growth. The first argues that economic policies should favour agriculture because it is a fundamental driver for starting economic growth in poor countries such as many in sub-Saharan African (Johnston and Mellor, 1961). The second synthesis, which focused on poverty, asserts that agriculture-centered development strategies are the most effective means of alleviating poverty (Dercon and Gollin, 2014). The third synthesis highlights that markets and institutions are fundamental entities that provide important gains to agriculture (Dercon and Gollin, 2014). Furthermore, Dercon and Gollin (2014) inserted two more discourse positions to these syntheses and based both on the importance of smallholder-based development strategies and on issues relating to the security and sovereignty of food. Also, post-Green Revolution theorists such as Hazell and Roell (1983), Haggblade et al. (1989; 1991), Hazell and Haggblade (1990), and Rosegrant and Hazell (2000) have all highlighted the role and importance of agriculture in rural development. For example, Rosegrant and Hazell (2000) showed that in countries where small-scale farming dominated agriculture, a positive impact of agricultural growth on rural development was higher than other countries where large-scale farming dominated. This further consolidates the crucial role of agriculture in Africa due to the widespread occurrence of rural poverty and small-scale farming on the continent (Diao et al., 2010).

Policies that favour agriculture in Africa are warranted. In this context, therefore, agricultural economic policies in Africa are being studied and reviewed to improve the agricultural sector, promoting rural development, and reducing poverty. For example, the New Partnership for Africa's Development (NEPAD), an economic development programme of the African Union (AU), which was officially adopted at the 37th session of the Assembly of Heads of State and Government in Lusaka, Zambia in July 2001, developed a special initiative called the Comprehensive Africa Agriculture Development Programme (CAADP) (Zimmermann et al., 2009). The rationale of developing CAADP was based on improving agricultural policies in Africa; to achieve sustainable agricultural growth and poverty reduction. Another subsidiary of NEPAD called the African Peer Review Mechanism (APRM) was established to provide major impacts on agriculture policies by improving governance in Africa (Zimmermann et al., 2009) with an operating assumption that improvement on the processes of policy-making will result in better policies and policy environments.

The efforts directed towards the improvement of the agricultural sector of Africa by these initiatives have been lauded, albeit with some provisions for improvement, and appear to have led to some successes (Zimmermann et al., 2009). However, the devastating impacts of pests and diseases on crop production have increased in recent times, represents a serious threat to agriculture in Africa (e.g. Ochilo et al., 2019). The impacts of these pests are particularly severe on impoverished smallholder farmers in rural areas who rely solely on agriculture for their food and livelihood means (Ochilo et al., 2019). This is typified by the impacts of the *T. absoluta* invasion in Africa. This thesis clearly showed the devastating effects of this pest on tomato production and concomitantly on livelihoods associated with tomato production in Eastern Africa. While the results obtained were alarming, they were not unexpected due to the rapid spread potential of the pest as reported in the literature. Adding to the contribution of tomato to food security and sustainable livelihoods, especially in impoverished rural households in Africa, discussed in the first chapter (Chapter 1) of this thesis, the rate of spread of *T. absoluta* and the impacts thereof were reviewed. The literature clearly showed that *T. absoluta* invasion in tomato agro-ecosystems in the Afro-Eurasia supercontinent has been rapid, achieving about 800 km increase in its range per annum (Desneux et al., 2011). This causes significant production losses in tomato across Africa, Asia, and Europe (Biondi et al., 2018; Desneux et al., 2010; 2011; Mansour et al., 2018), and there is new evidence showing that the indirect impacts of the pest on tomato-dependent livelihoods; especially in rural areas are as worse as

production losses (Chapter 2). This concluding chapter of this thesis provides insight into the socioeconomic impacts of *T. absoluta* invasion in Eastern Africa and the role of invasive pests in shaping human livelihoods. It further discusses the implications of the responses taken by tomato growers in the region to mitigate the impacts of this pest.

Globally, there is consensus on the use of integrated pest management (IPM), a strategy which aims to preserve the integrity of ecosystem functioning by conserving and promoting the natural mortality factors of pests through the combination of multifaceted pest management methods in a compatible manner for the management of agricultural pests (Barzman et al., 2015; Stern et al., 1959). There is evidence showing that the use of IPM increases yield in tomato and significantly reduces the application frequencies of synthetic pesticides such as parathionmethyl and abamectin, thereby conserving natural enemies and other beneficial organisms (Picanço et al., 2007). IPM systems are effective mainly because they incorporate ecological, economic, socioeconomic, and technical parameters in pest management (Dent, 2000; Pedigo, 1989). In this regard, Imenes et al. (1992) documented about 94% reductions in insecticide applications without damage to tomato yields and a significant increase in the number of species of natural enemies when IPM was employed. With the rationale of curbing the spread and ameliorating the socioeconomic impacts of *T. absoluta* in Eastern Africa and beyond, the potential of the co-evolved natural enemy, *D. gelechiidivoris*, of *T. absoluta* which was imported from South America into Kenya for classical biological control is discussed. Also, the implications of the potential synergism between *D. gelechiidivoris* and another biological control agent, *N. tenuis* for the management of *T. absoluta* in Eastern Africa, where the socioeconomic impacts of *T. absoluta* call for concerns are presented. This synergism between both biological control agents is particularly crucial because it may increase the overall biological control of the pest in Eastern Africa.

5.2 Spread of *Tuta absoluta* in Eastern Africa: distribution and infestation levels

In the first experimental chapter of this thesis (i.e. Chapter 2), the distribution of *T. absoluta* in Eastern Africa was determined. Further, the socio-economic impacts of the pests on tomato production and livelihoods associated with tomato production in the sub-region were evaluated. We mapped the distribution of *T. absoluta* in Eastern Africa and showed that the pest is widespread in Kenya, Sudan, Tanzania, and Uganda; the four countries sampled in the sub-region. These findings corroborate the literature in the introductory chapter of this thesis which

showed the high speed of spread of *T. absoluta* (Desneux et al., 2011), and the role of globalization and increase in international travel and trade in escalating the introductions of alien species in new environments throughout the world. There is no indication of either case abating. For example, following the first detection of *T. absoluta* in Sudan in June of 2010, results of the surveys conducted in chapter two showed that the pest has spread well over 3000 km in Eastern Africa in less than a decade. Furthermore, the investigations on the infestation levels of the pest, which was based on the number of infested tomato leaves and fruits in Kenya, revealed that *T. absoluta* is distributed with high infestation levels in the region. In Kenya, for example, fruits were routinely destroyed by tomato growers during harvesting as a result of the high infestations which caused fruits to rot by the action of opportunistic pathogens through the feeding galleries created by *T. absoluta* larvae. Tomato growers in Kenya reiterated that they normally incur huge yield losses in instances when insecticide applied against the pests was not effective or infestation levels required more than the usual insecticide application frequencies. This validates previous studies reporting the rapid rate of the spread, devastating impacts, and climatic suitability of *T. absoluta* in the new and potential areas of its invasion (Desneux et al., 2010, 2011; Tonnang et al., 2015). Although tomato growers in Kenya thought that the flight ability of the *T. absoluta* and human efforts such as transporting infested seedlings and fruits where the key drivers of the spread of the pest in Eastern Africa, these hypotheses were not the subject of this thesis, and therefore not tested. However, it is well-known that the aforementioned invasion drivers highlighted by the tomato growers in the region contribute to the success of biological invasions. This study suggests that containment will not be achievable.

To understand the high infestation level of *T. absoluta* in Eastern Africa, and the implications thereof, it is fundamental to examine the factors that determine the severity and success of invasion. There are several hypotheses of successful biological invasions (Richardson and Pyšek, 2006). In the majority of cases, the characteristics of the invader or the novel environments are implicated (Catford et al., 2009). A clear example is the propagule pressure hypothesis. Also known as introduction effort, the propagule pressure hypothesis asserts that introductions with high propagule pressure (a high number of individuals that are introduced in an event multiplied by the temporal frequency of these events) increase successful invasion chances as a result of high genetic diversity, continual supplementation, and the higher probability of introduction to suitable environment (Eppstein and Molofsky, 2007). Some

studies have argued that propagule pressure is the most fundamental driver of invasion (Crawley et al., 1996; Lockwood et al., 2005) but also crucial to understanding the idiosyncratic nature of biological invasions (Lockwood et al., 2005). This is because colonization can be due to a single propagule or require multiple introductions of multiple propagules (Colautti and MacIsaac, 2004). Furthermore, incessant or increasing introductions could serve as a buffer for temporarily unsuitable conditions and overcome genetic bottleneck events (Catford et al., 2009; Lockwood et al., 2005; Simberloff, 2009). This is mirrored in one of the two controversial hypotheses of naturalization by Darwin, which links phylogenetic relatedness between endemic communities and potential invaders with successful invasion probabilities (Darwin, 1859). That is, naturalization of closely-related introduced species is driven by appropriate niche adaptation as a result of habitat filtering, which creates a cascade of phylogenetic clustering or spatial pattern of or under dispersion of niches (Duncan and Williams, 2002). This indicates that biotic factors such as propagule pressure, human movement, global trade, and abiotic factors such as environmental suitability which promotes taxonomically related species in Eastern Africa are most likely also promote *T. absoluta* invasion in the region. These assertions are validated by the predictions of the potential distribution of *T. absoluta* in Africa (Guimapi et al., 2016). The cellular automata model by these authors showed that due to similarities in ecological indexes, the whole of Eastern Africa is suitable for the pest's invasion. Guimapi et al. (2016) also accurately predicted the year-by-year spread of *T. absoluta* in Africa. The predictions have since been validated by several first reports of the pest across the continent (e.g. Chidege et al., 2016; 2017; Visser et al., 2016).

The implications of the widespread distribution and high infestation levels of *T. absoluta* in Eastern Africa are serious. In this context, Parker et al. (1999) showed that the severity or impact of an invasive pest includes three fundamental dimensions: (i) geographical range; (ii) abundance; and (iii) the per-capita or per-biomass effect of the invader. The geographic range or distribution and abundance or infestation levels of *T. absoluta* recorded in Eastern Africa is alarming, as all 226 tomato agro-ecologies surveyed in the region had high infestation occurrences of the pest. This was the first indication of the potential detrimental socioeconomic impacts of *T. absoluta* on tomato production and livelihoods associated with the vegetable crop.

5.3 Socioeconomic impacts of *T. absoluta* in Eastern Africa: voices from Kenya

Interviews with tomato growers (respondents) in Kenya on the socio-economic impacts of the pest revealed that *T. absoluta* is the worst arthropod pest of tomato in Eastern Africa and a significant stressor of tomato-dependent livelihoods. Of course, this was expected due to the high infestation occurrence of the pest recorded in the region. However, to validate the respondents' summation of *T. absoluta* as the worst pest of tomato in the sub-region, assessment tests, using semi-structured questionnaires and oral interviews, on their knowledge of tomato pests showed that they had a good knowledge of invasive pests of tomato. Indeed, they described several pests of tomato or symptoms of infestations associated with specific pests such as Whiteflies. However, there was no incongruity in their classification of *T. absoluta* as the worst pest of tomato they have had to manage in the last decade. The interviews further revealed that despite the high application frequency of synthetic insecticides (a threefold increase following *T. absoluta* invasion), the impacts of the pest, including: tomato yield losses; livelihoods losses; reductions in household meals (due to the monetary losses incurred from yield losses); increases in debts incurred from farms; and school dropouts. The consequences of these direct and indirect impacts of the pest have resulted in exponential increases in the cost of tomato fruits in the region. Similar findings have been reported in Tanzania (Materu et al., 2016).

In the context of assessing the economic impacts of invasive pests, considerable effort has been directed towards developing management strategies that are effective to help prevent, understand, control, or ameliorate the impacts of such pests (Zimmermann et al., 2009). Previously, emphasis was placed on identifying the most cost-effective method of controlling the outbreak of an invasive pest (Evans et al., 2002). However, in recent times, the emphasis has been re-directed towards management benefits and costs of determining how best invasions can be managed (Evans, 2003). Bigsby and Whyte (2001) suggested two economic impacts categories of invasive pests, namely: direct and indirect impacts. According to Bigsby and Whyte (2001), direct impacts are entirely associated with the effects of the pest on the crop such as production losses, while indirect impacts are not host-specific, encompassing the general effects which are associated with the presence of a pest but not necessarily specific to the dynamics of pest (Bigsby and Whyte, 2001; Evans, 2003). This includes impacts on human and environmental health such as the irrational application of synthetic insecticides, market impacts such as changes in the perceptions and attitudes of consumers on a crop as well as

impacts on trade and economy (Evans, 2003). To simplify the understanding of two impact categories, the Food and Agriculture Organization (FAO) developed six impacts types which include: (i) production impacts (ii) price and market effects (iii) trade impacts (iv) food security and nutrition effects (v) human and environment impacts and (vi) financial costs impacts (FAO, 2001). Production impacts, which are considered as the most direct impacts on the economy, are concerned with the invasive pest which induces yield decline or production losses, while price and market impacts are directly proportional to the outbreak of a pest. These outbreaks could potentially re-shape the market size and elasticities of demand and supply of a crop produce (Evans et al., 2002; Evans, 2003). Trade impacts relate to the arrival or introduction of an invasive pest and the implication of its proliferation on production and trade losses, especially when entry bans are placed on the commodities from the affected country or, in less severe cases, when stringent entry precautionary measures are enacted. However, in either case, competitive trade advantages may be lost (Evans, 2003). Food and nutrition impacts show how invasive pests can affect food supply locally and how trade impacts could lead to a shortage of food. Although the understanding of an invasive pest's impact on human and environmental health are limited, there is evidence, however, that invasive pests cause serious impacts to the integrity of functioning ecosystems with serious socioeconomic consequences on human health and livelihoods. Although most studies easily calculate financial impacts such as control/eradication/prevention costs and the expected loss in the production of the crop (FAO, 2001), such an approach, has been classified as short-sighted, because in the majority of cases, the indirect effects arising from trade impacts could easily outweigh production loss impacts (Evans, 2003). In almost all crop pest invasions in Africa, these six impact categories have been affected, and it was documented concisely in the second chapter of this thesis.

Clearly, the socio-economic impacts of *T. absoluta* in Eastern Africa are serious and encompass the six impacts categories as identified by the FAO (2001). Nevertheless, the same could be said of some other pest invasions in Africa. For example, in Uganda, the mango industry is estimated to lose over $116 million annually due to the impacts of *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) infestations (Nankinga et al., 2014). In other instances, the impacts of tephritid fruit flies and their control costs have been estimated at US $3.2million per year in the Western Cape of South Africa (Barnes et al., 2002). In fact, with the recent invasion and establishment of *B. dorsalis* in the northern part of South Africa, a sevenfold increase in the initial estimated control cost has been predicted (Ekesi et al., 2016). Further to

these direct losses, several indirect losses due to quarantine restrictions have been documented. For example, following *B. dorsalis* invasion Kenya in 2003, the country lost the entirety of its avocado export market in South Africa. This led to over US $1.9 million loss in 2007 (Otieno, 2009), and over US $15.2 million as of 2014 (Ekesi et al., 2016). This ban by South Africa on fruits infested with *B. dorsalis* was also very serious on the economy of Mozambique, a very poor country losing over US $2.5 million every three weeks (Josê et al., 2013). Also, a wide range of fruits and vegetables, from several African countries, which were considered as potential hosts of *B. dorsalis* were banned for import into Mauritius, Seychelles, and South Africa (Ekesi et al., 2016). The impact of *B. dorsalis* on the African economy was further exacerbated by a USA Federal Order which banned the importation of fruits and vegetables (USDA-APHIS, 2008) and the European Union (EU) interceptions and destructions of tephritid fruitfly–infested fruits and vegetables imported from Africa increased dramatically from just 21 rejections in the whole of 2008 to 38 rejections in August 2009 (Ekesi et al., 2016).

Similar to the impacts of *B. dorsalis*, the financial losses suffered by Algeria, Libya, Morocco, and Tunisia due to the Mediterranean fruit fly *Ceratitis capitata* (Diptera: Tephritidae) have been estimated at US $67 million to 100 million per annum (IAEA, 1995). High infestation levels by this pest results in higher application frequencies of synthetic insecticides to curb its impacts. However, the introduction of insecticide residue thresholds across Europe compounds the problem of loss of export markets and constraints African exports. In a recent review, the financial losses caused by *C. capitata* in the horticultural industry in Africa due to the bans on exported goods was estimated at US $2 billion annually (Korir et al., 2015; Ekesi et al., 2016). These bans continue to have severe socioeconomic consequences on millions of people, especially rural dwellers, and smallholder farmers, who benefit from the horticulture industry in Africa (Ekesi et al., 2016).

A very recent serious case of invasion in Africa is the invasion by the Fall Armyworm (FAW), *Spodoptera frugiperda* (Lepidoptera: Noctuidae). This pest, native to the tropical and sub-tropical America, is currently considered as the most destructive crop pest in sub-Saharan Africa (Tambo et al., 2020). Following its first detection in West and Central Africa in 2016 (Goergen et al., 2016), FAW has spread into all countries, except Lesotho, in sub-Saharan Africa (FAO, 2019; Tambo et al., 2020), with devastating impacts on several crops (Montezano et al., 2018), particularly maize production (Rwomushana et al., 2018). Smallholder farmers in

Ethiopia and Kenya have reported a 47% reduction caused by FAW respectively (Rwomushana et al., 2018). Annual economic losses attributed to FAW in Ghana and Zambia have been estimated at US $177 million and US$159 million respectively (Rwomushana et al., 2018). In Zimbabwe, 58% FAW-induced maize yield reduction has been reported (Chimweta et al., 2020). In a nutshell, given the dietary and livelihood importance of maize in Africa (Shiferaw et al., 2011), the FAW invasion has caused significant losses in livelihoods of millions of poor smallholders across (Tambo et al., 2020). This remains the case to date.

The dynamics and magnitude of the socioeconomic impact of invasive species in Africa are alarming and significantly shape human livelihoods. *Tuta absoluta* invasion thus compounds this problem. This was reiterated in a recent review (see Shackleton et al., 2019), who showed that invasive species can be the the catalyst that induces transformations and disruptions, increasing the vulnerability of livelihoods thereby negatively impacting overall human well-being. Chambers and Conway (1992) and Scoones (1998) developed five domains of sustainable livelihoods, and Shackleton et al. (2019) underscored how invasive species can impact these domains. For example, in Eastern Africa, the invasion by *T. absoluta* has impacted all five domains by: (i) acting as a shock and stress; (ii) eroding capital; (iii) increasing its distribution range and impact due to porous sub-regional borders; (iv) inducing yield losses in tomato; and (v) increasing the cost of tomato production and human vulnerability; through frequent exposure to chemical pesticides. The findings in chapter two unraveled the impacts of *T. absoluta* in Eastern Africa, and it was, therefore, crucial to ameliorate these impacts which are particularly devastating on the sustainable livelihoods of smallholder tomato growers in the region. This prompted the importation of *D. gelechiidivoris* into Kenya, where pre-release evaluations of the parasitoids were conducted (Chapter 3).

5.4 A case for biological control of *Tuta absoluta* in Eastern Africa

The concept of biological control is reliant on the use of populations of an organism to cause a significant reduction in the population of another organism (Cock, 1985; Cock et al., 2010; van Lenteren et al., 2018; 2020). Biological control is one of the safest – in term of human and environmental health – and economically profitable methods of managing pests (Cameron et al., 1989; Cock, 1985; Cock et al., 2010; Mason and Huber, 2002; Neuenschwander et al., 2003; Waterhouse and Sands, 2001). This pest management approach has been employed for at least 2000 years (van Lenteren et al., 2018), but modern practices began just at the end of

the nineteenth century (DeBach, 1964; van Lenteren and Godfray, 2005; van Lenteren et al., 2020). The deleterious impacts of indigenous and alien pests in diverse natural and manipulated ecosystems can be managed using biological control agents such as parasitoids, predators, pathogens, herbivores, and antagonists (Cock et al., 2010). In principle, biological control can be carried out in four different ways namely: natural, conservation, augmentative, and classical biological control (Cock et al. 2010; Eilenberg et al., 2001).

Natural biological control which is generally acknowledged as an ecosystem service (Millennium Ecosystem Assessment, 2005), occurs naturally throughout the ecosystems of the world without anthropogenic intervention. In natural biological control, the densities of pest species are significantly suppressed by naturally occurring beneficial organisms. This type of biological control is unequivocally considered as the most important and greatest economic contribution of biological control to agriculture and biodiversity (Waage and Greathead, 1988). In conservation biological control, anthropogenic efforts are directed to protect and improve the performance of natural enemies which are naturally occurring (Mendes et al., 2011; Weller et al., 2002). Augmentative biological control largely involves mass-rearing natural enemies such as parasitoids, predators, and pathogens for mass releases with the rationale of providing an immediate control of a pest in crops having a short production cycle (i.e. inundative biological control) or to control several generations of a pest occurring in crops having a long production cycle (i.e. inoculative biological control) (Cock et al., 2010; Lorito et al., 2010; Parnell et al., 2016; van Lenteren, 2012). Classical biological control involves the exploration (usually in the naturally occurring range of a pest) and importation of natural enemies which are subsequently released in environments where the target pest is invasive. In the majority of cases, classical biological control often results in long term suppression of the pest's population and concomitantly with significant reductions in management costs (Cock et al., 2010; Turnbull and Chant, 1961).

Classical biological control was the first deliberate type of biological control practiced widely hence the name ''classical'' biological control (DeBach, 1964), and its numerous benefits encompass public health and environmental safety as well as significant reductions in control costs compared with mechanical and chemical methods of invasive pest management (Rao et al., 1971; Samways, 1988; Sweetman, 1958). In Africa, a historical overview of the benefits of classical biological control has been well documented (Greathead and Neuenschwander, 2003).

For example, the successful control of the cassava mealybug *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae) by the exotic parasitoid *Apoanagyrus lopezi* (De Santis) (Hymenoptera: Encyrtidae) clearly articulates these benefits. Results of this successful classical biological control revealed that *A. lopezi* significantly reduced yield losses caused by *P. manihoti* and the cumulative economic benefits after 40 years was estimated at US $ 9.4 billion, with a yearly benefit of US $ 23.5 million (Zeddies et al., 2001).

Although there have been some cases in which deliberate introductions and releases of exotic biological control agents have caused significant problems (Howarth, 1991; Louda et al., 2003; Klopfer and Ives, 1997; Lynch et al., 2001), these cases, have been very few (Cock et al., 2010). To ensure that the introductions of exotic natural enemies would not impose threats on the integrity of native flora and fauna; the major criticism of classical biological (Howarth, 1991), several stringent measures such as risk assessments on non-target species have been recommended (Bigler et al., 2006; Nowell and Maynard, 2005; van Lenteren et al., 2006). Initially, many biological control practitioners thought that this would impede new programmes, but Kairo et al. (2003) have documented no decreases in the annual number of new natural enemies being released albeit some delay in applications may occur. This process, generally called "pre-release evaluation", is now considered quintessential for the success of classical biological control (Kuhlman et al., 2006; Sands and van Driesche, 2004; van Lenteren et al., 2006). The benefits of classical biological control enumerated above, and the lack of effective endemic natural enemies of *T. absoluta* in Eastern Africa served as the rationale for the importation of *D. gelechiidivoris* into Kenya.

In the context of the need for pre-release evaluations of an exotic natural enemy for classical biological control, as highlighted above, the second experimental chapter of this thesis (Chapter 3: focused on providing biological control (classical biological control using a parasitoid) for the management of *T. absoluta* in Africa. Here, the parasitic potential and key aspects of the biology of *D. gelechiidivoris* was subjected to pre-release evaluations under quarantine conditions at the International Centre of Insect Physiology and Ecology (*icipe*), Nairobi, Kenya. However, before the laboratory pre-release evaluations, it was prudent to understand certain crucial aspects of parasitoid-host interactions. For example, following emergence, female parasitoids often arrive in alien habitats and separated from a host population (Vinson, 1976). This means that to propagate, a female parasitoid must first seek and locate a suitable

environment (Salt, 1935), and subsequently find a suitable host in that environment (Vinson, 1976). This process is complex but dependent on environmental and host factors (Laigo and Tamashiro, 1966), and it is believed that the chemical and physical components in the environment are crucial in guiding parasitoids to host habitats (Vinson, 1976). Immediately a suitable host habitat is located by a female parasitoid, she then proceeds, in a systematic manner, to searching for suitable hosts (Laigo and Tamashiro, 1966; Vinson, 1976). This complex process which leads to successful parasitism is divided into five steps (i) host habitat location; (ii) host location; (iii) host acceptance; (iv) host suitability; and (v) host regulation (Doutt, 1959; Flanders, 1950; Fiske, 1910; Salt, 1935; Smith, 1957).

In the review by Vinson (1976), the first three of these steps (i.e. host habitat location, host location, and host acceptance) were categorized into a broad heading called host selection. However, in another review, Vinson and Iwantsch (1980) included the fourth step; host suitability, to the process of host selection because host suitability is fundamentally concerned with the host as an oviposition site or reproduction sink as well as the parameters which affect the development of the parasitic stage of the parasitoid. Consequently, the suitability of a host to support the development of a parasitoid represents an additional crucial factor required for successful parasitism (Vinson and Iwantsch, 1980).

Many host pest species have an intrinsic ability to mount a cellular immune response, against parasitism, called encapsulation (Rizki and Rizki, 1984; Strand and Pech, 1995). In this process, the parasitoid egg is first recognised as a foreign entity or non-self (Kraaijeveld et al., 2002). This recognition leads to a storm of cytokines and other proteins which mediate the aggregation of blood cells called haemocytes, forming a multilayered capsule, on, and around the egg (Strand and Pech, 1995). Subsequently, a separate class of haemocytes or crystal cells and enzymes of the phenoloxidase-cascade induce the deposition of melanin around the haemocyte-egg aggregate (Strand and Pech, 1995). In the majority of cases, the parasitoid egg dies if the deposition of melanin leads to a closed and blackened capsule (Nappi et al., 1995; Nappi and Vass, 1998). This is probably due to starvation or asphyxiation, or possibly due to the toxic substances which are produced from the capsule (Nappi et al. 1995; Nappi and Vass, 1998). In other cases, where the host survives, the encapsulated eggs are normally visible as a black dot in the abdomen (Kraaijeveld et al., 2002). This indicates that the ability of a parasitoid to develop within a host typically depends on its ability to regulate the physiology of the host

(Vinson and Iwantsch, 1980). In this regard, several parasitoid species have specialized mechanisms to counter the physiological defensive mechanisms of host species. For example, several parasitoid species attacking the fruit fly *Drosophilia melanogaster* (Meigen, 1830) (Diptera: Tephritidae) can mount several counter-defence mechanisms against encapsulation (Kraaijeveld et al., 2002). For example, the egg of *Asobara tabida* (Nees) (Hymenoptera: Braconidae) has developed proteinaceous filaments in its chorion which makes the eggs sticky, hidden, and inaccessible in host tissues, thereby evading the circulating heamocytes in the host heamolymph (Kraaijeveld and van Alphen, 1994; Eslin et al., 1996). Conversely to the passive counterdefence mechanism of *A. tabida*, species of the genus *Leptopilina* such as *Leptopilina heterotoma* (Thomson) (Hymenoptera: <u>Figitidae</u>) and *Leptopilina boulardi* (Barbotin, Carton and Kelner-Pillault) (Hymenoptera: <u>Figitidae</u>) actively suppress the immune system of their hosts by injecting virus-like filaments into the host (Rizki and Rizki, 1990; Dupas et al., 1996). It is believed that these pathogenic filaments gain entry into the haemocytes of the host and induce apoptosis (Rizki and Rizki, 1990).

In the third chapter of this thesis, crucial aspects of the host selection process of *D. gelehiidivoris* were studied. These aspects included the host stage preference as well as the acceptability and suitability of *D. gelechiidivoris* with *T. absoluta* as host. Also, some aspects of the parasitoid's life-history traits such as potential lifetime fecundity, egg maturation dynamics, and intrinsic rate of natural increase were disentangled. The concluding synthesis on the parasitic potential of *D. gelechiidivoris*, in chapter three emphasized the high parasitic capacity of *D. gelechiidivoris* on *T. absoluta* and there was no record of *D. gelechiidivoris* egg encapsulation, indicating its ability in regulating the physiological defence mechanisms of *T. absoluta*.

Dolichogenidea gelechiidivoris oviposited preferentially into early larval instars (1st and 2nd) of *T. absoluta*. This oviposition preference for early host stages is generally characteristic of the majority of braconid parasitoids in the Microgastrinae sub-family (Whitefield et al., 2018). However, the evolutionary traits, merits, and trade-offs associated with this reproductive strategy remains unclear (Whitefield et al., 2018). *Dolichogenidea gelechiidivoris* females also parasitized the late larval instars (3rd and 4th) of the host and completed its immature development in all four larval instars of the host. That is, all four host larval instars produced reproductively viable females. These findings clearly showed that *T. absoluta* is a suitable host

of *D. gelechiidivoris* and in conformity with the second hypothesis of this study ("*Dolichogenidea gelechiidivoris will accept T. absoluta larvae for oviposition and the host instar larvae will support the juvenile development of the parasitoid*" Chapter 1). An explanation for this successful parasitism could be attributed to *D. gelehiidivoris* ability to evade the internal defence mechanisms of *T. absoluta*. Indeed, the ability to evade the internal defence mechanisms of hosts is fundamental to successful parasitism and several parasitoid species have specialized evolutionary strategies such as carefully placing their progeny (i.e. eggs) on or inside certain tissues of their host such as ganglion and fat body. In other instances, parasitoids may deposit eggs in the host stage(s) which confer adequate protection to their progeny. This is mainly because hymenopteran parasitoids are reliant on the nutrients of their hosts (Sequeira and Mackauer, 1992a; Vinson and Iwantsch, 1980), and the immature stages of parasitoids, especially the larvae, rely solely on the ability of their mother to accurately evaluate the suitability of hosts for their development (Vinson, 1976; Vinson and Iwantsch, 1980).

Even though an insect host is considered suitable for the development of a parasitoid species (Mackauer, 1973; Salt, 1940), there is evidence showing that variations occur in the quality and quantity of resources resident in the different host developmental stages (Vinson and Iwantsch, 1980; Sequeira and Mackauer, 1992b). For example, in instances where a parasitoid attacks several life stages of a host, as is the case of *D. gelechiidivoris* with *T. absoluta* as host, the nutritive quality for larval development varies with host size or stage (Vinson, 1976; Vinson and Iwantsch, 1980). This means that female parasitoids should preferentially choose the host stage of a host species with the greatest return to their reproductive performance (Charnov and Skinner, 1985; Sequeira and Mackauer, 1994). This is the concept of the optimality theory postulated by Bell (1991) and Stephens and Krebs (1986). However, host size is also a crucial factor with which parasitoids use in assessing host quality (Van Alphen and Jervis, 1996). In many koinobiotic parasitoids, a size-fitness relationship is produced due to host growth – indicative of continuous feeding by the host – during parasitoid larval feeding and development (Sequeira and Mackauer, 1992b). This variation occurs within-host instar rather than by the size of the host at parasitization (Sequeira and Mackauer, 1992b). Consequently, host size does not equate to optimality. Put simply, the biggest host may not necessarily provide the greatest nutritional quality to the developing parasitoid (Harvey et al., 1994; Sequeira and Mackauer, 1994). This has been confirmed in many studies on koinobiont parasitoids, showing that the

strategies of host instar selection differ from idiobiotic parasitoids (see Henry et al., 2005 and references therein). For example, the parasitoid-host interaction between the parasitoid *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae) and its host, the pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), Sequeira and Mackauer (1994) produced a non-linear variation in the life-history parameters of the *A. ervi* when developing in each of the four different host larval instars, with the greatest offspring fitness returns resulting from the second instar hosts.

Perception of host value by a female parasitoid, defined as the perceptual assessment of a host's quality by a parasitoid female (Mackauer et al., 1996), is crucial in host selection or host suitability assessments by a female parasitoid (Henry et al., 2008; Vinson and Iwantsch, 1980). Mackauer et al. (1996) showed that following the location of a potential host in the host habitat, a female parasitoid evaluates the nutritive quality and suitability for the development of its progeny through behavioural activities such as antennation and ovipositor probing. In some cases, a female parasitoid may assign an erroneous value to a host or host stage due to its inexperience with the host. In other instances, erroneous host values may be assigned by inaccurately ranking the hosts with imperceptible physiological defences against parasitism (Harvey and Strand, 2002; Henter and Via, 1995; Kraaijeveld et al., 2002). In either case, however, it leads to a decision to oviposit in a host or host stage which could significantly beleaguer the survival chances and reproductive potential of the progeny (Harvey and Strand, 2002; Henter and Via, 1995; Kraaijeveld et al., 2002). Henry et al. (2005) explored the disparity between host quality and host preference of *A. ervi* and the foxglove aphid *Aulacorthum solani* (Harris) (Homoptera: Aphididae) and showed that the host's early larval instars (1st and 2nd) produced the greatest reproductive progeny fitness returns. However, when presented with each of the four host larval instars, *A. ervi* preferentially oviposited into the older larvae (3rd and 4th) of the host, disregarding their reductions in suitability for larval development and thereby reducing its reproductive performance (Henry et al., 2005). This suggests that sometimes, mothers do not always know best even amongst parasitic parasitoid species.

In the case of *D. gelehiidivoris*, the decision of the parasitoid to oviposit in early larval instars of the host did not prove costly to its reproductive performance and progeny fitness returns. In assessing the host suitability and progeny reproductive returns, no cases of egg encapsulation were recorded in each of the four host larval instars, and the egg load of females emerging from

the 2nd, 3rd, and 4th larval instars of the host were not significantly different, indicating no reductions in its reproductive performance. However, in females reared on the first larval instar of the host, there was a reduction in egg load but not significant enough to be considered as serious reductions because the parasitic rates of females reared from each of the four host larvae instars were similar. A likely explanation, albeit not tested, for the choice of younger instars could be the energy expended when attempting to parasitize the host, with older larval instars which are much larger than early larval instars. For example, in the behavioural assays conducted, *D. gelechiidivoris* females spent considerably longer period antennating, probing, and wrestling with the older larval instars of *T. absoluta* than the early instars. This suggests that it may be energy-cost effective to parasitize early instars than late instars, at least in *D. gelelchiidivoris* females.

Generally, egg production traits of parasitoids that are considered crucial in improving congruence between egg and the availability of host encompass the cumulative stem line oocytes, which predetermines the maximum lifetime potential fecundity, known as oogonia, the maximum number of fully chorionated eggs (i.e. mature eggs) that can be accumulated within the ovarian tubes at a given time, the dynamics of egg maturation, mature eggs size as well as the propensity for, and rate of, egg resorption (Jervis and Kidd, 1986; Jervis et al., 2001; Price, 1975). Among these characteristics, one crucial outcome of the interactions is the cumulative of oocytes which a female carries, the fraction of the maximum potential lifetime egg complement that is mature when she emerges into the environment varies greatly among parasitoid taxa (Jervis et al., 2001). The investigations carried out on the ovarian physiological status (proovigenic vs synovenic) of female *D. gelechiidvoris* revealed that it is a weakly synovigenic species, defined as high egg load following adult female eclosion albeit with some increase with age (Flanders, 1950). Synovigeny is prominent amongst the majority of Braconidae parasitoid species (Jervis et al., 2001). Conversely, proovigeny, which refers to having the maximum lifetime potential egg load complement mature upon emergence is rare among parasitoid wasps (Flanders, 1950; Jervis et al., 2001).

It is well known that the success of parasitoids is correlated with the number of suitable hosts encountered and the number of eggs available (Ellers et al., 2000; Jervis et al., 2001). This indicates that the allocation of resources to survival and reproduction is subjected to strong selective pressure (Ellers et al., 2000). Host searching incurs energy and time costs, and once

a host is located, the parasitoid should be able to use this opportunity (Ellers et al., 2000). This means that a parasitoid should develop a dynamic egg maturation strategy to reduce the risk of egg limitation; that is, being void of eggs while hosts can still be encountered (Ellers et al., 2000; Heimpel and Rosenheim, 1998). Following the review of Heimpel and Rosenheim (1998), the risk of egg limitation in parasitoids has become well recognized and several studies have investigated this phenomenon. For example, Weisser et al. (1997) simulated the life history of the aphid parasitoid *Aphidius rosae* Haliday (Hymenoptera: Braconidae) based on measurements of host encounter rates, lifetimes, and travel times. These authors discovered that the distribution of realized fecundities was highly skewed and that a significant proportion of the parasitoids did not reach their potential fecundity in their lifetime.

We noted that the concentration of resources towards the early adult reproductive life of *D. gelechiidivoris* may have affected the longevity of the parasitoid. Jervis et al. (2001) described this phenomenon as a trade-off associated with the intensification of resources for early parasitoid adult life which is characteristic of many weakly synovigenic and all proovigenic parasitoids. This is the theory of life-history (concentration of 'reproductive resources' towards early adult life incur trade-offs) (Jervis et al., 2001). It postulates that parasitoids that greatly invest resources in oogenesis before adult life will not live long enough to encounter sufficient hosts for their eggs. On the other hand, if they invest greatly in life span, they will be egg limited; finding significantly more hosts than eggs available (Ellers et al., 2000; Heimpel and Rosenheim, 1998). The optimal allocation strategy must occur between these extremes (Ellers et al., 2000). Put simply, life span is negatively correlated with the proportion of mature oocytes following emergence (Jervis et al., 2001). Therefore, proovigenic wasps are expected to have shorter lifespan than synovigenic species (Flanders 1950).

In synovigenic parasitoids, resources allocated to reproduction can indeed be adjusted during life (see Ellers et al., 2000 and references therein). To a large degree, parasitoids that are synovigenic have the ability of achieving a more accurate match of egg load and oviposition opportunities, as is reflected in their higher lifetime reproductive success and the higher percentage of eggs laid (Ellers et al., 2000). Regardless of the trade-off in longevity, the oviposition rate of the *D. gelechiidivoris* was high and one female was capable of parasitizing a high number of *T. absoluta* larvae in her lifetime because it can still live long enough to achieve a high net reproductive rate *Ro* of 39 daughters per female. This means that the females

of *D. gelechiidivoris* can adjust their reproductive resources; depending on host availability, to demonstrate prolific oviposition rates. However, in stochastic environments, the optimal egg load of synovigenic parasitoids can exceed the expected number of hosts encountered (Ellers et al., 2000). This indicates that their relative fecundity is not significantly different from proovigenic parasitoids (Ellers et al., 2000; Jervis et al., 2001).

In the third and final experimental chapter of this thesis we investigated the nature of the interaction between *D. gelechiidivoris* and another biocontrol agent, the generalist zoophytophagus predatory bug *Nesiodiocoris tenuis* (Reuter) (Hemiptera: Miridae) with *T. absoluta* as host. Generally, unlike specialists, predators that are generalist frequently engage in intraguild predation (Polis and Holt, 1992; Rosenheim et al., 1995; Rosenheim, 1998). This typically involves feeding not only on other predators but also on parasitoids (Brodeur and Rosenheim, 2000; Snyder and Ives, 2001), thus exacerbating prey outbreaks when the interaction is significant (Rosenheim et al., 1993, Snyder and Ives, 2001, Snyder and Wise, 2001). Through strong intraguild predation, herbivore damage to crops is increased (Snyder and Wise, 2001). Despite these limitations, generalist predators have been reported as successful biological control agents in several cropping systems, including tomato agro-ecologies (Chailleux et al., 2013; Riechert and Bishop, 1990, Snyder and Wise, 2001). In the case of *T. absoluta* control using generalist predators and specialist parasitoids, the interaction between *Macrolophus pymaeus* Wagner (Hemiptera: Miridae) and *Stenomesius japonicus* Ashamed (Hymenoptera: Eulophidae) has been reported to exhibit complementary functional traits (Chailleux et al., 2017). This validated the previous study by Chailleux et al. (2013), showing that *M. pymaeus* and oophagous parasitoids of the Trichogrammatidae (Hymenoptera) (Chailleux et al., 2013) we compatible for combine control of *T. absoluta*, as both natural enemies significantly reduced populations of the pest. However, Chailleux et al. (2013) noted intraguild predation by *M. pygmaeus* on *Trichogramma achaeae* Nagaraja and Nagarkatti, but reiterated that the risk of the predation was dependent on the larval developmental stages of *T. achaeae* in *T. absoluta* eggs. They further recommended the use of both natural enemies because the combination of both natural enemies had more efficacies against the pest than the predator alone.

The rationale for this third experimental chapter was to evaluate the possibility of using both natural enemies for the control of *T. absoluta* in Africa. This was important because *N. tenuis*

is widespread throughout Africa (Mansour et al., 2018). Therefore, the potential interaction between both natural enemies, prior to the release of *D. gelechiidivoris*, had to be understood. Indeed, there have been several criticisms on the use of multiple biocontrol agents without pre-release evaluations prior to releases (Denoth et al., 2002; Myers et al., 1989), hence the reason for proper assessments (Morin et al., 2009). Furthermore, this interaction assessment study was particularly crucial to understand if *N. tenuis*; a voracious predator of *T. absoluta* eggs which can also prey on the host larvae, would inflict intraguild predation on *D. gelechiidivoris*. Concurrent and sequential releases each of both natural enemies were made in the test arena and we used different densities of *N. tenuis* (1, 2 and 4) to determine its potential intraguild predation on *D. gelechiidivoris*. Overall, there was no indication of significant predation by *N. tenuis* on both parasitized and unparasitized *T. absoluta* larvae, suggesting that regardless of the sequence of the combination of both natural enemies and the density of predator, *N. tenuis* did not inflict intraguild predation on *D. gelechiidivoris* which was mainly attributed to the fact that *N. tenuis* host feeding on *T. absoluta* larvae was low and insignificant, and also too little to significantly affect the progenies of *D. gelechiidivoris*. This was the first indication of a potential combination of both biocontrol agents.

Subsequent evaluations – impact assessment studies – revealed that when both biocontrol agents were combined, the density of *T. absoluta* population was reduced significantly more than when either agent occurred alone. This proved that *N. tenuis* and *D. gelechiidivoris* can be used for the control *T. absoluta* because, under normal ecological scenarios in tomato agro-ecologies, all life stages of *T. absoluta* occur at any given time, indicating that both biocontrol agents would attack its preferred host stage (i.e. host eggs for *N. tenuis* and host larvae for *D. gelechiidivoris*), thereby limiting the possibility of intraguild predation. This could be considered a synergistic interaction between both biocontrol agents and agrees with the third hypothesis of this thesis: "*The predation on* T. absoluta *larvae by* N. tenuis *will inflict intraguild predation on* D. gelechiidivoris *and reduce the performance of the parasitoid*": Chapter 1. However, further testing under open-field and greenhouses are required. Clearly, there is a potential for combining *D. gelechiidivoris* and *N. tenuis* for the control of *T. absoluta* in Africa. In this context, augmentative releases of both biocontrol agents can be made across different tomato agro-ecologies in the sub-region to reduce the infestation levels of the pest.

5.5 Recommendations

This thesis was limited in numerous aspects. First, the surveys of the distribution of *T. absoluta* were limited to four countries in Eastern Africa. Therefore, the distribution of the pest in the rest of Eastern Africa is unknown. Although tomato growers in Kenya served as the representation for the region, it would be prudent to include the voices of other tomato growers in the rest of the region, to ascertain a better understanding of the devastating impacts of *T. absoluta*, especially on rural livelihoods in the region. Furthermore, other fundamental aspects of the biology of *D. gelechiidivoris* such as its host specificity, interactions with endemic parasitoids, and temperature effects on its life-history traits are not known. Increasingly, the role of facultative symbiotic organisms in biological control is gaining significance. It would be interesting to identify the microbiome community of *T. absoluta* and investigate their potential role in the interactions between the pest and the exotic parasitoid.

The role of biotic and abiotic factors such as anthropogenic movements, trade, temperature, and humidity in facilitating the distribution of *T. absoluta* was highlighted in this thesis. It was shown that the occurrence and suitability of these factors are more or less the same across Eastern Africa (Tonnang et al., 2010). However, this thesis showed the distribution of *T. absoluta* in only four countries in the region, suggesting that *T. absoluta* is probably widespread in other Eastern African countries not surveyed like Ethiopia, Eritrea, Rwanda, and Somalia. A clear understanding of the pests' distribution in the region is fundamental for a concerted regional alliance. Therefore, further surveys should be carried out throughout the rest of Africa. These surveys should also include a socioeconomic impact assessment component to understand the role of *T. absoluta* in shaping smallholder tomato livelihoods in the region as well as a proper documentation of the economic losses on tomato production caused by the pest in Eastern Africa.

This thesis, in chapter three, disentangled some fundamental pre-release aspects of *D. gelechiidivoris* such as host stage preference, acceptability, and suitability. However, testing the host range of an exotic natural enemy before releases is crucial to predicting any potential risk of negative impacts on non-target species in the novel environment (Barratt et al., 2006). Results of the host specificity testing would either validate the data in this thesis, supporting the release of the parasitoid, or provide new evidence on the potential risk of *D. gelechiidivoris* introduction. In either case, an informed decision on the release of *D. gelechiidivoris* can be

made. There is a consensus that phylogeny and ecological similarities are valuable starting points for predicting and assessing the field host range of a parasitoid (Hoddle, 2004; Kuhlmann et al., 2006; van Lenteren et al., 2006). Therefore, closely related Gelechiidae species such as and species that share ecological habitats and niches with *T. absoluta* such as would be good starting points for testing the host specificity of *D. gelechiivoris* in Eastern Africa.

Chapter four of this thesis showed the importance of investigating the nature of interactions between two or more natural enemies of a pest. The combination of both *D. gelechiidivoris* and *N. tenuis* provided a more effective control of *T. absoluta* population. Therefore, sampling for naturally occurring parasitoids and predators of *T. absoluta* in Eastern Africa should be made to raise healthy colonies of each of the natural enemies. Subsequently, assays investigating the nature of the interactions amongst these biocontrol agents should be conducted. This could potentially increase the biocontrol of *T. absoluta* in the region and beyond. Indeed, this combined biocontrol strategy is currently providing some relief of the pests' pressure in North Africa (see Mansour et al., 2018, and references therein).

It is well established that of a suite of abiotic factors influencing the biology, ecology, and population structure (dynamics) of pests and their natural enemies, temperature is the most significant (Dixon et al., 2009). Reaumur (1735, 1736) almost 300 years ago, first recognized that living organisms cannot develop below certain temperature thresholds and that the cumulative temperature required for complete development is fairly constant, notably, referred to as degree days nowadays (Furlong and Zalucki, 2017). This indicates that different organisms (including natural enemies and their host/prey) differ in their thermal limits and range of temperature for survival, development, mobility, and reproduction (Roy et al., 2002). Organisms living under extremely low or high-temperature environments must either circumvent or tolerate these conditions to ensure their survival, and mechanisms by which they evade these harsh conditions have been documented (see reviews of Bale, 2002; Hodkinson, 2005). In recent times, several studies have furthered our understanding by disentangling the relationship between the physiological and evolutionary responses of organisms and their thermal environment (e.g. van der Have, 2002; Jarosik et al., 2002, 2004; Dixon et al., 2009). Because insects are ectotherms, and their body temperatures are a significant reflection of the range of temperatures they experience in their local environment (Furlong and Zalucki, 2017).

Understanding thermal thresholds of *D. gelechiidivoris* will help in developing an effective biological control measures against *T. absoluta*, whereby the optimum temperature (T_{opt}) for rearing and appropriate time for release within the year will be identified based on temperature conditions. This indeed, becomes important when the environmental temperatures are greater than the T_{opt}, (Furlong and Zalucki, 2017).

Symbiotic bacteria are commonly associated with insects and their influences in shaping the ecology and evolution of their host species are increasingly gaining relevance (McFall-Ngai et al., 2013).Some bacterial symbionts colonize populations of their hosts through vertical transmissions from mother to progeny (Moran, 2006), and may attain a high occurrence in host populations (Smith et al., 2015). Facultative symbionts are not generally required for the survival or reproduction of their host, but frequently confer conditional costs and benefits by mediating host traits such as nutrition and reproduction (Douglas, 2015; 2009). In other instances, they can influence resistance against adverse biotic and abiotic conditions such as greater thermal tolerance, wider host plant range, and defense against specialized natural enemies such as fungal pathogens and parasitoid wasps (Guay et al., 2009, Oliver et al., 2014). In elucidating the role of facultative endosymbionts in negating the success of biological control, the journal *Biological Control* in a recent special issue titled "When insect endosymbionts and plant endophytes mediate biological control outcomes" published papers which clearly articulated that facultative symbionts alone can compromise biological control programmes involving the use of biological control agents such as parasitoids and fungi (e.g. Desneux et al., 2019; Hopper et al., 2019; Otero-Bravo and Sabree, 2019; Vorburger, 2019). Therefore, metagenomic studies of the symbionts of *T. absoluta* are warranted to understand the diversity of the resident facultative endosymbionts in this pest and their potential role in the interaction between *T. absoluta* and *D. gelechiidivoris*.

5.6 Closing synthensis

This thesis provided novel insights into the spread and impacts of *T. absoluta* in Eastern Africa as well as the potential of an exotic parasitoid, *D. gelechiidivoris*, for classical biological control of the pest in Africa. The socioeconomic impacts of *T. absoluta* in Eastern Africa are serious, encompassing significant losses both in tomato yield and livelihood returns, and there is no indication of these impacts abating. However, the use of indigenous voices (local tomato growers) in assessing the impacts of *T. absoluta* on livelihoods improved the understanding of

the local perceptions, impacts, and management of the pest in the region and also provided a platform to educate the locals on the need for biological control of the pest. Therefore, it is recommended that *D. gelechiidivoris* should be released in Kenya, following release permits from the Kenya Plant Health Inspectorate Services (KEPHIS), and subsequently across Eastern Africa. This is supported by the suitability of *T. absoluta* as host for *D. gelechiidivoris* and the high parasitic capacity of *D. gelechiidivoris*. Also, there is a potential for combined biocontrol of *T. absoluta* using *D. gelechiidivoris* and *N. tenuis*. The combined efficacies of both natural enemies improved the overall control of the pest. Therefore, exploring this potential could result in reduced yield losses in tomato induced by *T. absoluta*.

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